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Production of Heuchera and Coleus

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According to the USDA ERS, 2008 receipts from greenhouse and nursery sales ranked fourth among agricultural commodities in Maine and seventh in the nation. Greenhouse and nursery plant production relies on the availability of quality water for irrigation and, often involves the use of supplemental lighting to enhance the quality and growth of the plants being produced. Increasing energy costs and more frequent water shortages associated with changing demographics, water use legislation, and climate factors have inspired growers to consider more sustainable approaches to utilizing resources such as water and energy. Precise, crop-specific water and light recommendations are essential to help growers make more sustainable production decisions.

Two investigations were conducted to determine the water and light requirements for *Heuchera americana* 'Dale's Strain' (heuchera), an herbaceous perennial prized for its variegated foliage. Both investigations used a capacitance sensor automated irrigation system to accurately manage substrate volumetric water content (θ). In the first study, the substrate was maintained at one of eight θ ranging from 0.15 to 0.50 $L \cdot L^{-1}$ while the

second experiment assessed performance under four daily light integrals (DLI) (7.5, 10.8, 14.9, and 21.8 $mol \cdot m^{-2} \cdot d^{-1}$) with θ remaining constant.

Total leaf area in plants grown at the highest θ was more than twice that observed in plants grown at the lowest θ. Shoot dry weight also responded positively to increasing θ, although θ greater than 0.35 $L \cdot L^{-1}$ did not continue to yield significantly greater dry weights. DLI caused dry weight, leaf area, maximum width and leaf count to increase quadratically. Increases in dry weight and leaf area appeared to reach saturation at 10.8 $mol \cdot m^{-2} \cdot d^{-1}$, while width and leaf count were greatest at 14.9 $mol \cdot m^{-2} \cdot d^{-1}$. Increasing DLI to 21.8 $mol \cdot m^{-2} \cdot d^{-1}$ negatively impacted leaf area, leaf count and width, but did not result in lower dry weights. Specific leaf area ($cm^2 \cdot g^{-1}$) and petiole length of the uppermost fully expanded leaf decreased with increasing DLI. Measures of fluorescence, net photosynthesis, light response curves, and carbon dioxide response curves indicated no physiological differences among plants grown under different water or light treatments. Water use efficiency (WUE) based on dry weight and water applied ($g \cdot L^{-1}$) decreased with increasing θ and DLI while WUE based on leaf gas exchange was not influenced by θ and increased with increasing DLI. From this information, we suggest θ be kept somewhere between 0.35 and 0.5 $L \cdot L^{-1}$ and DLI in the range of 11 to 15 $mol \cdot m^{-2} \cdot d^{-1}$ for optimal heuchera production.

Solenostemon scutellarioides (coleus), another crop valued primarily for its ornamental foliage, has traditionally been used as a shade plant, but many new cultivars are suitable for full sun. Many have noted a variation in leaf coloration when coleus is

grown under different light levels, but to our knowledge, no one had quantified this difference. Therefore, two cultivars of coleus were grown under four DLIs (2.9, 3.8, 5.8, and 10.0 $mol \cdot m^{-2} \cdot d^{-1}$) to determine how DLI influenced morphology and leaf variegation. Both cultivars coleus had optimal growth and more variegation (i.e. less green area) under 10.0 $mol \cdot m^{-2} \cdot d^{-1}$.

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LITERATURE REVIEW

1.1 *Heuchera americana* L.

Heuchera americana L., a member of the Saxifrage family, is characterized by a collection of coarsely-toothed basal leaves which are rounded or broad usually with 5 lobes and a heart shaped base. Leaves are evergreen with leaf flushes primarily occurring in spring (Wells, 1989), but have also been reported to occur in fall as well (Skillman et al., 1996). Leaf blade size and petiole length are noted to differ depending on plant vigor and the environmental conditions upon leaf emergence (Wells, 1989).

Creamy flowers are borne on loose panicles above the foliage starting in late spring or early summer, depending on the climate in which it is growing. Roots form a shallow taproot system, with the taproot measuring approximately 1cm in diameter and roughly 4-8cm long. Adventitious roots developing from the shortened (1-2cm) stem compose a significant portion of the root mass in mature plants (Wells, 1989).

The natural distribution for *H. americana* ranges from Georgia northward to Ontario and from Indiana eastward to New York (USDA, 2009; Wells, 1989). Native individuals are most commonly observed in rocky, dry, deciduous understory habitats (Armitage, 1989; Cullina, 2000; Heims and Ware, 2005, Skillman et al., 1996). These habitats are characterized by seasonal fluctuations in light and temperature. Light levels in these settings, measured in mols of photons received over a given area during the course of 24 hours, typically range from approximately 1-2 $mol \cdot m^{-2} \cdot d^{-1}$ in the summer months to around 11 $mol \cdot m^{-2} \cdot d^{-1}$ in the winter (Skillman et al., 1996).

Many popular cultivars have been developed from this species because of its potential for vivid venation characteristics and silvering effects. Variations of foliar color include gold, white, caramel, chartreuse, lemon yellow, scarlet, and burgundy with an equal amount of diversity in the variegation patterns.

The common name for *H. americana*, 'alumroot', refers to its taste and strong medicinal qualities. Pharmaceutical alumroot is an astringent and antiseptic that has been used to treat wounds, ulcers and diarrhea among other ailments (Heims and Ware, 2005). Heuchera is also referred to as 'heuchera', 'rock geranium' or 'coral bells', the latter reflecting on the coral flower color of the first ornamental cultivars derived from *H. sanguinea* (Heims and Ware, 2005).

Selected by nurseryman Dale Hendricks, *H. americana* 'Dale's Strain' has blue-green foliage with striking veins ranging in color from sliver, or greenish purple to red. Leaf margins tend to have a thin band of gray-green coloring, contrasting the traditionally silver-green area between the leaf veins. Its mounding habit reaches a height and spread of approximately 45-60 cm. Reliable hardiness zones range from 4 to 7 (North Creek Nurseries, 2007).

H. americana 'Dale's Strain' can be propagated by seed or through division. Seed propagated plants can be variable in appearance and parent plants should remain isolated as they hybridize freely (Heims and Ware, 2005). Seeds should be surface sown onto a germination mix in plug trays and later transplanted into a soilless potting mix for finished production (Kujawski and Davis, 2001). Cuttings require an axillary bud and are most successful when taken in spring (Cullina, 2000). Heuchera is also frequently propagated through tissue culture (Cullina, 2000). Fertility recommendations for

growing plants in the genus *Heuchera* are to apply 150-200 mg/L nitrogen during every other irrigation event (Ball Horticultural Company, 2009).

The demand for native plants in the horticultural market has increased dramatically over the past several years. Driving forces behind this trend include educational outreach and effective marketing campaigns such as the *American Beauties* program. *American Beauties* is a marketing campaign promoting the use of native plants in the landscape resulting from the collaboration of the National Wildlife Federation, Pride's Corner Farm, and North Creek Nursery (National Wildlife Federation, 2009). Consistent increases have also been observed in the perennial foliage plant market. Gardeners have come to appreciate perennials with unique leaf coloration because they provide visual interest in the garden throughout the season. Heuchera has had the benefit of both positive trends. It is commonly used in perennial borders, container plantings, and as a small-scale groundcover (Armitage, 1989; Cullina, 2000; Heims and Ware, 2005).

1.2 *Solenostemon scutellariodes* (L.) Codd

Coleus (*Solenostemon scutellariodes* (L.) Codd) is a diverse and enormously popular group of ornamental foliage plants that have been enjoyed by plant enthusiasts for over a century (Armitage, 2001; Rogers and Hartlage, 2008). As a member of the mint family, coleus is characterized by square stems, opposite leaves and bilabiate flowers (Rogers and Hartlage, 2008). Cultivars are primarily selected for foliage characteristics such as size, shape and color. Preference is also given to selections that produce few flowers and maintain a dense growth habit (Stack, 2009). The uniquely

colored foliage of coleus can be found throughout the landscape in garden beds, containers, and hanging baskets. Leaves of coleus are either composed of a single color or are a distinctly variegated combination of two or more colors including burgundy, green, pink, coral, yellow, orange, and dark purple.

Although traditionally recommended as a shade plant, many newer cultivars of coleus have been reported as being suitable for full sun (Armitage, 2001; Rogers and Hartlage, 2008; Stack, 2008). Light is known to influence leaf coloration in some cultivars of coleus (Bin Liu, personal communication). Recommended light levels for coleus production have been reported by multiple authors (Ball Horticultural Company, 2009; Faust, 2003). However, to our knowledge, no study has quantified the influence of light on leaf coloration in this genus.

Foliage of 'Kong Red' coleus is characterized by a deep burgundy center with a dark green margin, while 'Wizard Coral Sunshine' coleus has a bright coral center edged with burgundy surrounded by a light green margin. In a field trial assessing the relative performance of 79 coleus cultivars in Northern US full sun conditions, 'Wizard Coral Sunrise' was grouped in the category deemed least suitable for full sun conditions while 'Kong Red' was among those considered to be good candidates for full sun gardens (Stack, 2009). These conclusions were based on the relative amount of sunscald that appeared on the upper foliage of the plant throughout the growing season. Average outdoor daily light integrals in this region during the summer growing season range from approximately 30 to 45 $mol \cdot m^{-2} \cdot d^{-1}$ (Korczynski et al., 2002).

1.3 Light

1.3.1 Measuring and managing light

Light is one of the most highly managed environmental parameters in plant production. It can vary in quality (wavelength), duration (daylength), and quantity; all of which can have significant impacts on plant morphology, physiology, growth, and reproduction (Faust, 2003). The influence of varying the quantity of photosynthetically active radiation a plant receives will be considered here. This variable is usually discussed in terms of an instantaneous measure or a cumulative measure over time. Instantaneous measures of light provide information about the intensity of light received at a given moment, whereas cumulative measures give a picture of how much light energy is provided over a given day (Fisher and Runkle, 2004). The latter is referred to as daily light integral (DLI) and is measured in moles of photons of light within the wavelengths of light that are used in photosynthesis per square meter per day ($mol \cdot m^{-2} \cdot d^{-1}$).

Growers often enhance the DLI available to a crop through the use of supplemental lighting. Depending on the light requirements of the crop being grown, this approach can significantly reduce the amount of time it takes to yield a finished product, allowing the growers to increase the number of plants produced over a single production season. On the other hand, some crops may not respond positively to higher light levels and may even require that light levels be reduced (Faust, 2003). In these situations, DLI can be minimized by using screening materials that block out a certain percentage of light without influencing the quality of light received (Heins and Runkle, 2004). Both

supplemental lighting and screening materials can be costly to purchase, install, and operate (Fisher and Both, 2004; Heins and Runkle, 2004). Therefore, it is important that growers become familiar with the specific light requirements for the crops being grown so that they can determine if it is economically beneficial to invest the time, effort, and money involved in managing light.

1.3.2 Light influences plant morphology and physiology

Plant growth is a function of the environmental factors in which it is exposed to. When other abiotic factors such as nutrients and water are not limiting, plant growth is dictated by the amount of light available, the morphological, anatomical, and biochemical ability for a plant to absorb the light available, and the physiological capacity for the species to utilize the light received (Taiz and Zeiger, 2006).

Plants employ a number of strategies for survival and success in the specific light levels of their native habitats. Shade adapted species frequently have morphological features that maximize the potential for light absorbance such as greater leaf area per unit mass and crown architecture that minimizes self-shading (Evans, 1999; Pearcy and Yang, 1998). For example, the herbaceous understory plant *Adenocaulon bicolor* Hook. (trail plant), effectively manages leaf arrangement, petiole length, leaf angle, and leaf size in a manner that results in an optimal design for light capture (Pearcy and Yang, 1998).

Anatomical changes, such as low internal self-shading via changes in mesophyll structure, and reorientation of chloroplasts allow for greater light capture in shade adapted plants (Evans, 1999, Taiz and Zeiger, 2006).

Plants adapted to low light generally invest more resources in photosynthetic light harvesting antennae and fewer resources towards electron transport and Calvin cycle enzyme production and activity. Relatively low respiration rates are also characteristic of shade-adapted species. This strategy allows plants to more easily obtain a positive carbon balance under relatively low light levels (Henry and Aarssen, 1997; Pearcy and Yang, 1998; Walters, 2005).

Unlike animals, plants are not able to move to a better location when environmental conditions, such as light, change in a manner that may negatively impact their potential for growth and survival. Inefficient use of light and even damage to the photosynthetic apparatus can occur when plants adapted to low light become exposed to periods of high light (Taiz and Zeiger, 2006). Species exposed to seasonal changes in light in their native locale often have the ability to limit damage that can occur under high light and may also be able to adjust their photosynthetic capacity to take advantage of the additional light resources available (Skillman et al., 1996).

Heuchera is an excellent example of a plant capable of photosynthetic acclimation. When overstory trees lose their leaves in the winter, heuchera are exposed to light levels 3-10 greater than those observed in summer months. When photosynthetic activity was monitored on a monthly basis, investigators observed that heuchera had the ability to utilize the additional light received in the winter months by increasing photosynthetic capacity (Skillman et al., 1996). It has been suggested that the observed changes in photosynthetic capacity could be attributed, in part, to a shift in nitrogen allocation favoring light-harvesting functions over photosynthetic enzymes and electron transport in summer foliage (Henry and Aarssen, 1997; Skillman et al. 1996). This

proposed change in resource allocation within the photosynthetic apparatus would allow plants to efficiently capture more light in the summer when light is limiting and, in the winter, be able to utilize the energy from increased available light for carbon assimilation. In a study a few years later, Skillman and Osmond (1998) reported that nitrogen availability influenced the capacity for *H. americana* to acclimate to high light. Nitrogen deficient plants growing in high light conditions had a lower quantum yield of incident light, reduced chlorophyll content, and lower estimates of maximum photosynthesis compared to plants with adequate nitrogen resources.

Rothstein and Zak (2001) observed similar trends with *Viola pubescens* Ait. (downy yellow violet) and *Tiarella cordifolia* L. (foamflower). Both plants had greater concentrations of rubisco under higher light conditions and increased chlorophyll concentration when light was less available. The same investigation gave evidence that supported the hypothesis that leaf persistence may limit the capacity for a plant to acclimate to changing light conditions. Plants with more frequent leaf turnover, such as the downy yellow violet, are more capable of adjusting photosynthetic capacity throughout the year compared to plants with more persistent foliage, such as the foamflower (Rothstein and Zak, 2001). Skillman et al., (1996) also observed this phenomenon when comparing photosynthetic plasticity of heuchera, with a leaf life span of 6-7 months, to *Hexastylis arifolia* (Michaux) Small, with a leaf life span of 12-13 months.

1.3.3 Light influences leaf coloration

Plants often alter pigment concentration in response to changes in light availability and light quality (Taiz and Zeiger, 2006). The proposed function of these pigments in leaf tissue has been the source of much discussion (Chalker-Scott, 1999; Smillie and Hetherington, 1999; Steyn et al., 2002). Much of the literature has supported a photoprotective function, with higher anthocyanin concentrations reducing photoinhibition and photo-oxidative damage (Steyn et al., 2002). Following this theory, anthocyanins, the pigment responsible for most of the reddish purple coloration in ornamental plants such as smokebush (*Cotinus coggygria* Scop. 'Royal Purple') and purple fountain grass (*Pennisetum setaceum* (Forssk.) Chiov. 'Rubrum' and 'Red Riding Hood') has been noted to increase with increasing amounts of light (Beckwith et al., 2004; Oren-Shamir and Levi-Nissim, 1997). This pigment is also primarily responsible for the red to purple coloration observed in the ornamental plant coleus (*Solenostemon scutellarioides* L. Codd) (Lamprecht et al., 1975). The coloration in coleus has been noted to change according to the light level in which it has been growing (Bin Liu, personal communication), the visual implications of changes in anthocyanins have not been quantified for coleus up to this work.

DLI can also influence leaf variegation. Examples of foliage plants that become more variegated when grown under more light include English ivy (*Hedera helix* L.), pothos (*Epipremnum aureum* Bunt. E. pinnatum), and cast-iron plant (*Aspidistra elatior* 'Variegata' Bl.) (Pennisi et al., 2005; Stamps, 1995). Conversely, the leaves of variegated cultivars of radiator plant (*Peperomia obtusifolia* L.) and dracaena (*Dracaena*

sanderana hort. Sander ex Mast.), have more variegation when plants are grown under less light (Shen and Seeley, 1983; Vladimirova et al., 1997).

1.4 Water

1.4.1 Managing water

Recent data from the United States Geological Survey indicate that, between 2000 and 2005, there was an 8% reduction in water withdrawals associated with irrigation. Irrigation ranks second, just below thermoelectric power, among all water consumption categories, accounting for 31% of total water used in the U.S. in 2005. Much of the reduced consumption has been attributed to more efficient irrigation practices such as sprinkler and drip irrigation replacing less efficient methods, such as flood irrigation (Kenny et al., 2009). These changes in watering practices are permitting growers to yield more crops while using significantly less water. Another benefit to using more efficient methods is the reduced volume of effluent that is emitted into local ground and surface waters. Agricultural effluent has been known to be a source of potentially harmful levels of nitrates and phosphates, which can have serious impacts on both environmental and human health (Pierzynski et al., 2005). More and more states are considering, or have already implemented, legislation regarding water management in various agricultural sectors including horticulture (Lea-Cox and Ross, 2001).

Automated irrigation systems are a vital part of most greenhouses and nurseries; they lessen labor costs and limit excess water use. Quite often, these systems are turned on and off manually or by using timers. An alternative to these methods is automating irrigation based on measurements from sensors. Sensor driven systems can be divided

into three major groups depending on the parameters measured: greenhouse environmental conditions, plant water status, or substrate water status (Burnett and van Iersel, 2010).

The system based on substrate water status described in Nemali and van Iersel (2006) uses capacitance sensors; it is accurate, and has the potential to yield no leachate (Burnett and van Iersel, 2008). Plants may be grown with as little as 1 liter of water for the entire growing cycle (van Iersel et al., 2006). Accuracy and minimal leaching is heavily dependent on knowledge of precise water requirements for the crop being grown. Therefore, if systems driven by substrate water status are to be implemented on a broad scale, it is necessary to develop a database of substrate volumetric water content (θ) requirements for all greenhouse grown crops. Previous evaluations of the sort have been performed for the perennial *Gaura lindheimeri* Englem. & Gray 'Siskiyou Pink' (Burnett and van Iersel, 2008).

Increased market interest in plants tolerant of relatively low water availability has prompted several studies evaluating the influence of water deficit on the growth and physiology of commercially available ornamental plants (Cameron et al., 2008; Franco et al., 2008; Nemali and van Iersel, 2008; Niu et al., 2006; Prevete, et al., 2000; Sanchez-Blanco, 2009; Starman and Lombardini, 2006; Zollinger et al., 2006). Drought tolerance strategies vary from species to species and even among cultivars. Tolerance of water stress also depends on the degree and intensity of stress imposed as well as a plants previous exposure to drought (Kramer and Boyer, 1995; Pospíšilová and Dodd, 2005). A number of different methods have been used to implement water deficit for research purposes (Burnett et al., 2005; Burnett et al., 2006; Cameron et al., 2008; Eakes et al.,

1991; Franco et al., 2008; Niu et al., 2006; Sánchez-Blanco et al., 2009; Starman and Lombardini, 2006; Zollinger et al., 2006). Few studies have contrasted plant response to degrees of water deficit using an irrigation system such as the one described by Nemali and van Iersel (2006) (Burnett et al., 2008; Nemali and van Iersel, 2008).

Numerous studies have suggested that growing plants with more conservative amounts of water can enhance their future success in potentially water-limited retail and landscape settings (Cameron et al., 2008, Franco et al., 2006, and Franco et al., 2008). Using less water during production can promote a number of plant characteristics that improve water uptake and allow tissue water status to be maintained both of which will be described in more detail later. This cultural technique can help ensure that the economic and environmental resources invested in producing plants aren't lost during the final stages of plant sales.

1.4.2 Water influences plant morphology and physiology

Leaf expansion is one of the morphological features most influenced by water deficit. Increasing cell size is a function of both the yield threshold of the cell wall and turgor pressure within the cell. Turgor pressure alone can only result in transient, or elastic, changes in cell size and plants are often able to maintain turgor during mild water deficit. However, cell expansion can occur when turgor increases happen in conjunction with a relaxation of the cell wall. Cell wall extensibility is generally negatively influenced by water stress due to changes in pH that can occur in the cell wall solution (van Volkenburg, 1999). Extensibility is greatest when the pH is slightly acidic, therefore increases in pH associated with drought can cause an increase in the yield

threshold of the cell wall (Taiz and Zeiger, 2006). Leaf area plays a significant role in whole plant growth in response to water deficit because plants with reduced leaf area are generally not as able to capture as much light for photosynthesis as those with a higher leaf expansion rate (Taiz and Zeiger, 2006). Therefore, reduced total leaf area and dry weight in plants exposed to drought is, in large part, the result of both decreased cell wall extensibility and relatively low whole plant photosynthetic activity due to less light interception.

Reduced cell expansion limits other means of plant growth including plant height and internode length. These features can also result in lower light capture which can, in turn, reduce growth rate. Several ornamental crops including *Pelargonium x hortorum* L. (bedding geranium), *Salvia farinacea* Benth. (mealycup sage), and *Plumbago auriculata* Lam. (plumbago) have been noted to have reduced leaf area, height, and dry weight when exposed to limiting water conditions (Niu et al., 2006; Sánchez -Blanco et al., 2009; Starman and Lombardini, 2006).

Reduced dry weights observed in plants growing with low water availability are also greatly due to reduced photosynthetic activity. Drought stress is known to limit photosynthesis through both the reduction of CO_2 movement to the site of photosynthesis and the impairment of metabolic functions (Bjorkman and Powles, 1984; Zhou et al., 2007). The movement of CO_2 from the atmosphere to the site of photosynthesis is influenced by three major points of resistance: the boundary layer, stomata, and mesophyll. The latter can be further broken down into three sources of resistance within the leaf: intercellular air space resistance, cell wall resistance, and liquid intracellular resistance (Flexas et al., 2008).

One of the most well known strategies for maintaining plant water status is the closure of stomata. Abscisic acid (ABA) is the primary hormone responsible for signaling stomatal closure. Production of ABA is stimulated by water stress, although it has also been observed in tissue of well-watered plants. ABA is synthesized in both root tissue and shoot tissue and stomatal sensitivity to ABA can be influenced by many factors including leaf age and abiotic environmental characteristics (Pospíšilová and Dodd, 2005). Stomata in some plants exposed to prolonged periods of drought may not recover to fully open status or may be more sensitive to ABA, making plants more tolerant of future drought stress events (Franco et al, 2008; Pospíšilová and Dodd, 2005).

Resource allocation may also influence shoot dry weight. Many plants allocate a greater amount of biomass towards root growth relative to shoot growth in response to low substrate water content (Mohr and Schopfer, 1994). A review by Poorter and Nagel (2000) suggested that many species follow this trend.

Physiological responses to drought are usually only apparent under very low tissue water potentials (Mohr and Schopfer, 1994). In an attempt to find trends in photosynthetic response to drought stress, Flexas and Medrano (2002) concluded that metabolic impairment occurs primarily when stomatal conductance is less than 0.05-0.1 $mol \cdot H_2O \cdot m^{-2} \cdot s^{-1}$, regardless of species or leaf water status.

1.5 Assessing physiological responses to light and water

Instantaneous gas exchange measures can provide useful information regarding the rate of net photosynthesis (A_N), stomatal conductance (g_s), and the rate of transpiration (E) (Long et al., 1996). These measures can be very useful in expressing the

rate of activity at a given time under a given set of environmental conditions. However, instantaneous measures do not provide a picture of the factors that characterize the actual rate of carbon assimilation such as dark respiration, quantum efficiency, carboxylation efficiency, light saturated electron transport rate and more. An explanation of the light response curve, carbon dioxide response curve, and fluorescence measures that help provide a more complete picture of the factors limiting photosynthetic capacity will be described here.

Developing a response curve tracking A_N at incremental intensities of photosynthetically active radiation (Q) (i.e. a light response curve or A_N-Q curve) can provide useful information regarding the degree to which certain physiological parameters are limiting photosynthesis. In the early part of the curve, when A_N continues to increase in response to higher Q, it is possible to estimate the efficiency in which a unit of light is used to assimilate a unit of carbon dioxide (CO_2). This measure is referred to as the quantum efficiency (QE). The portion of the curve where increasing Q no longer results in a significant increase in A_N represents the CO_2 limited phase. At this point, further increases in A_N are limited by the carboxylation efficiency of rubisco in the Calvin cycle, which is generally limited by Rubisco availability or activity, or CO_2 availability (Taiz and Zeiger, 2006). The bending degree, or convexity (k) of the transition between the light limited and CO_2 limited portions of the curve also provides insight into the relative efficiency of the photosynthetic apparatus. Convexity values reflect the degree of the light gradient within the leaf. Lower k values are observed when the light gradient is relatively high due to instances of self-shading. Photosynthesis in the range of light at this transition point is most efficient when k is closest to 1.

Measuring A_N under saturating light conditions at various CO_2 concentrations inside the leaf (C_i) can also provide key information about the biophysical and biochemical limitations to photosynthesis (Long and Bernacchi, 2003; Taiz and Zeiger, 2006). Using C_i instead of atmospheric CO_2 (C_a) concentrations eliminates the inclusion of stomatal and boundary layer resistances, allowing investigators to estimate limitations occurring solely within the leaf (Long and Bernacchi, 2003). Increasing CO_2 concentrations inside the leaf results in a curvilinear response in A_N similar to that observed with light. In the carbon dioxide response curve (A_N-C_i), when C_i is low, the carboxylation activity of Rubisco (V_c) is the primary factor limiting A_N. Therefore, the initial slope of the A_N-C_i curve is an indication of the rate of carboxylation activity mediated by the enzyme Rubisco. Multiplying the slope of this portion of the curve, by the C_i concentration where the curve begins to saturate results in the maximum rate of carboxylation (V_{cmax}). Regeneration of the Calvin cycle substrate ribulose-1,5-bisphosphate (RuBP) is the limiting factor when further increases in C_i fail to yield significant increases in A_N. The light saturated rate of electron transport (J_{max}) that is primarily responsible for the regeneration of RuBP can be quantified by estimating the slope of the saturated portion of the curve (Long and Bernacchi, 2003; Taiz and Zeiger, 2006).

Mesophyll resistance (g_m) to CO_2 movement can be influenced by plant response to DLI. g_m can be broken down into three sources of resistance within the leaf: intercellular air space resistance, cell wall resistance, and liquid intracellular resistance (Flexas et al., 2008).

The higher the g_m, the more inaccurate the estimations of V_{cmax} and J_{max} will be, as mesophyll resistance will result in lower carboxylation efficiency and possibly reduce the efficiency of RuBP regeneration. The influence of g_m should be, at least, acknowledged as a possible factor influencing estimates of metabolic function (Flexas et al., 2008).

Another method that is used to assess photosynthetic capacity is chlorophyll fluorescence. When a unit of light (photon) is either absorbed directly by a chlorophyll molecule, or its energy is transferred to a chlorophyll molecule from an accessory pigment, the chlorophyll molecule is left in a very unstable, excited state. The highly excited chlorophyll molecule quickly loses some energy in the form of heat moving it to a more stable, lower excited state. At this point, the remaining excess energy in the chlorophyll molecule has three general fates, all of which return the pigment to its lowest energy (ground) state. One option is referred to as non-photochemical quenching and is often characterized by a loss of energy in the form of heat or the transfer of energy to another molecule. The second option is to utilize the energy for photosynthesis. The third possible fate entails having the photon re-emitted in a lower energy state (as some of the energy was lost in the initial heat loss stage). This process is known as fluorescence and is often measured in order to assess damage to the photosynthetic apparatus (Taiz and Zeiger, 2006). One of the most commonly reported measures of fluorescence (Fv/Fm) represents the maximum efficiency of PSII. Non-stressed plants typically have a Fv/Fm value of 0.83 (Jones, 1992) whereas Fv/Fm values range somewhere around 0.5-0.7 in stressed plants (Skillman and Osmond, 1998). This

measure is typically correlated with QE, but factors such as electron transport efficiency may negatively influence QE, yet not reflect differences in Fv/Fm (Taiz and Zeiger, 2006)

1.6 Water use efficiency

Water use efficiency (WUE) has been of interest to researchers and growers for over three centuries (Sinclair, 1984) and, quite possibly, even longer. Put simply, WUE is a measure of crop yield per unit water use. One definition of WUE offered by Sinclair (1984) shows the diversity in how this measure can be assessed by stating that WUE is "a ratio of biomass accumulation, expressed as carbon dioxide assimilation, total crop biomass, or crop grain yield, to water consumed expressed as transpiration, evapotranspiration, or total water input to the system". Sinclair (1984) also noted the temporal differences in how WUE is assessed which can measured as instantaneous, daily, and seasonal representations of WUE. Such a comprehensive definition demonstrates that numerous methods can be utilized over various periods of time to determine the efficiency in which water is used by plants and that the methods used should be carefully chosen to support the research goals that need to be fulfilled.

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CHAPTER 2:

INFLUENCE OF SUBSTRATE WATER CONTENT AND DAILY LIGHT INTERGRAL ON GROWTH AND MORPHOLOGY OF *HEUCHERA AMERICANA*

2.1 Abstract

The efficient use of water and energy is a key factor in improving sustainability in horticulture. Automated irrigation systems based on substrate water status can reduce water use, lower costs associated with labor and energy, improve plant quality and health, and eliminate the output of harmful effluent associated with excessive irrigation. Supplemental lighting can help growers increase their profit margins by reducing the amount of time it takes to produce a marketable crop. In order to use these tools wisely, it is important that growers have a keen understanding of the light and water requirements of the crops being grown. Two studies were conducted to determine the water and light requirements for the native herbaceous perennial *Heuchera americana* L. 'Dale's Strain' (heuchera). In one study, the substrate was maintained at one of eight substrate volumetric water contents (θ) ranging from 0.15 to 0.50 $L \cdot L^{-1}$. A second experiment evaluated the effects of four daily light integrals (DLI) (7.5, 10.8, 14.9, and 21.8 $mol \cdot m^{-2} \cdot d^{-1}$) on heuchera growth and morphology while θ remained constant. Total leaf area and shoot dry weight were both positively correlated with θ (P=0.0036 and 0.009, respectively). Dry weight was not significantly enhanced by θ higher than 0.35 $L \cdot L^{-1}$. However, leaf area was significantly greater in the highest θ set point (0.5 $L \cdot L^{-1}$) compared to plants growing in all of the lower θ set points. DLI had a quadratic influence on dry weight, leaf area, maximum width and leaf count. Increases in dry

weight and leaf area appeared to reach saturation at 10.8 $mol \cdot m^{-2} \cdot d^{-1}$, while width and leaf count were greatest at 14.9 $mol \cdot m^{-2} \cdot d^{-1}$. Increasing DLI to 21.8 $mol \cdot m^{-2} \cdot d^{-1}$ negatively impacted leaf area, leaf count and leaf width, but did not result in lower dry weights. Specific leaf area ($cm^2 \cdot g^{-1}$) and petiole length of the uppermost fully expanded leaf decreased with increasing DLI. We recommend that θ be maintained somewhere between 0.35 and 0.5 $L \cdot L^{-1}$ and DLI should be kept in the range of 11 to 15 $mol \cdot m^{-2} \cdot d^{-1}$ for optimal heuchera production.

2.2 Introduction

Increasing economic and environmental pressures on the horticultural industry have prompted many discussions on the topic of sustainability over the past several years (Hall et al., 2009; Krug et al., 2008; Mattson et al., 2009). Krug et al. (2008) defined sustainable horticultural practices as methods that reduce environmental impact of production conserve resources, and support a stable community, while maintaining high productivity. Such practices include the use of efficient irrigation technology and the proper use of supplemental lighting to conserve water and reduce energy use. In order to maximize the efficient use of both, it is necessary to have a keen understanding of the specific light and water requirements of the crops being grown.

Recent innovations in automated irrigation technology allow growers to minimize water consumption and eliminate effluent that could contain harmful levels nitrates and phosphates (Burnett and van Iersel, 2008; Nemali and van Iersel, 2006; Pierzynski et al., 2005). One system monitors substrate volumetric water content (θ) using capacitance sensors located within the growing substrate. These sensors relay information back to a

computer that triggers an irrigation valve to open if θ is too low (Nemali and van Iersel, 2006). A study comparing the efficiency of this method of irrigation to cyclic irrigation based on timers revealed that, over the course of a month, the cyclic irrigation method used approximately 30 gallons of water per plant compared to only 1 gallon per plant in the system based on θ (Arguedas et al., 2008).

Growing plants with less water can enhance their future success in potentially water-limited retail and landscape settings (Cameron et al., 2008, Franco et al., 2006, and Franco et al., 2008). This production technique helps ensure that the economic and environmental resources invested in producing plants aren't lost during the final stages of plant sales. Reducing plant available water can also limit unwanted stem elongation in certain crops, allowing growers to supplement or forgo expensive growth regulator applications that are normally used to produce more compact plants (Burnett et al., 2005, Burnett et al., 2006).

Interest in plants tolerant of low water availability has prompted several studies evaluating the influence of water deficit on the growth and physiology of a number of commercially available ornamental plants (Cameron et al., 2008; Franco et al., 2008; Nemali and van Iersel, 2008; Niu et al., 2006; Prevete, et al., 2000; Sánchez-Blanco, 2009; Starman and Lombardini, 2006; Zollinger et al., 2006). There are many different ways in which plants respond to water stress. Lower leaf areas and shortened internodes have been observed in many species including *Pelargonium x hortorum* L. (bedding geranium), *Salvia farinacea* Benth. (mealycup sage), and *Plumbago auriculata* Lam. (plumbago) (Niu et al., 2006; Sánchez -Blanco et al., 2009; Starman and Lombardini, 2006). Plants such as geranium and *Silene vulgaris* (Moench.) Garcke shift growth

allocation towards more relative root growth compared to shoot growth (Franco et al., 2008; Sánchez -Blanco, 2009). Reduced dry weight has been noted in *Scaevola aemula* R. Br. (fan flower), *Petunia* x *hybrida* (petunia), *Cineraria maritime* L. (dusty miller) and plumbago (Niu et al, 2006; Starman and Lombardini, 2006).

A number of different methods have been used to implement water deficit for research purposes. In one study, plants were allowed to dry down to visible wilt before rehydration (Eakes et al., 1991). Zollinger et al. (2006) subjected plants to water deficit by watering them once every 2 or 4 weeks. Investigators in other experiments applied drought stress by refraining from watering until containers reached a certain target weight (Niu et al., 2006; Sánchez-Blanco et al., 2009; Starman and Lombardini, 2006). These methods can be time consuming and may result in greater fluctuations in the actual substrate volumetric water content (θ) compared to other methods of regulated deficit irrigation. Further, studies that rely on container weight to indication soil water status may not account for changes in root and/or shoot mass that may influence container weights significantly, resulting in a significant source of experimental error. Few studies have contrasted plant response to continuous drought stress using an irrigation system such as the one described by Nemali and van Iersel (2006) (Burnett et al., 2008; Nemali and van Iersel, 2008). If irrigation systems triggered by substrate water status are to be implemented on a broad scale, it is necessary to determine crop-specific volumetric water content (θ) requirements.

The irrigation system Nemali and van Iersel (2006) developed also provides an excellent means of keeping θ stable during studies assessing plant response to light level. If an irrigation system is not responsive to changes in soil water status due to increased

evaporative demand, water stress can occur in plants exposed to high light or, conversely, plants growing in low light may experience periods of excessive water supply (Burnett and van Iersel, 2010).

Light is limiting for growth for many greenhouse grown crops. Reduced light levels can result in lower shoot biomass, reduced leaf and flower production, and a lower total leaf area (Faust et al., 2005; Oh et al., 2009; Pennisi et al., 2005). Growers combat this issue by providing supplemental lighting to increase the photosynthetically active radiation a plant receives throughout a day, also known as daily light integral (DLI). This increases the growth rate of many species, thus reducing the time it takes to produce a marketable crop and increasing the number of crops growers produce throughout a season (Faust, 2003; Fisher and Both, 2004). For example, when including the reduction in light transmission associated a greenhouse structure and glazing, mean daily light integrals during the spring production season in the Northeast can range as low as 8-12 $mol \cdot m^{-2} \cdot d^{-1}$ (Fisher and Runkle, 2004). Meanwhile, the minimum recommended DLI for high quality *Viola* (pansy) production is 18 $mol \cdot m^{-2} \cdot d^{-1}$ (Faust, 2003). Supplemental lighting can be expensive to purchase, install, and operate. According to cost estimates presented in Fisher and Both (2004), the expenses associated with increasing the DLI by approximately 3.5 $mol \cdot m^{-2} \cdot d^{-1}$ would be around $5.64 per square foot of growing space.

Enhancing light levels may not result in a more marketable, fast growing crop. For example, increasing DLI beyond 19 $mol \cdot m^{-2} \cdot d^{-1}$ resulted in no further increases in dry weight of *Begonia* x *semperflorens-cultorum* L. (begonia) and *Impatiens wallerana* L. (impatiens) and increasing DLI beyond 11.5 $mol \cdot m^{-2} \cdot d^{-1}$ yielded no additional increase in leaf count or number of flowers in *Cyclamen persicum* Mill. (Faust et al., 2005; Oh et al.,

2009). Therefore, it is important that growers know whether it is economically beneficial to provide crops with additional light.

Heuchera americana L. (heuchera) is an evergreen herb native to deciduous understory habitats in the Eastern U.S. (Heims and Ware, 2005; USDA, 2009). It is composed of basal leaves that are palmately lobed and have a heart-shaped base. Numerous cultivars have been developed from the species because of its potential for vivid variegation and silvering effects (Heims and Ware, 2005). The increasing popularity of native plants as well as the continued appreciation for foliage crops has provided heuchera with a stable foothold in the ornamental plant market. To our knowledge, little more than anecdotal information has been reported regarding the specific light and water requirements for this species (Cullina, 2000; Heims and Ware, 2005). Therefore, the objectives of this study are to quantify the optimal θ and daily light integral required to produce *Heuchera americana*.

2.3 Materials and Methods

2.3.1 Experiment 1: Water

The cultivar chosen for this study was *H. americana* 'Dale's Strain', a popular selection having silver and green foliage with veins ranging in color from deep green to purple (Heims and Ware, 2005). Pre-vernalized plugs were obtained from a commercial nursery (Bluestone Perennials, Madison, OH) and were transplanted into nursery containers (3.8 L) using a commercial soilless substrate (Fafard 2P, 60% peat:40% perlite (v/v), Fafard, Agawam, MA). All containers were evenly watered to container capacity immediately after planting and were subsequently fertigated with a continuous liquid feed

of 200 $mg \cdot L^{-1}$ N solution (Peters EXCEL 15N-2.2P-12.45K Cal-Mag, The Scotts Co., Marysville, OH). Beginning 10 June, 2008, the fertilizer solution was changed so that 100 $mg \cdot L^{-1}$ N was provided by the previously mentioned commercial fertilizer and 100 $mg \cdot L^{-1}$ N was applied in the form of calcium nitrate ($CaNO_3$).

The water study began on 5 May 2008 and continued for 56 days. Growing substrate in each container was maintained at one of eight θ set points (0.15, 0.2, 0.25, 0.3, 0.35, 0.4, 0.45, or 0.5 $L \cdot L^{-1}$) using a capacitance sensor-automated irrigation system (Nemali and van Iersel, 2006). In this system, capacitance sensors (EC-5; ≈ 5cm x 2cm, Decagon Devices, Pullman, WA) were set to measure the voltage of the substrate every five minutes. Sensors relayed the voltage to a CR-10X datalogger (Campbell Scientific, Logan, UT) where the voltage measurement was used to calculate θ using a substrate specific calibration equation (θ = voltage × 1.7647 – 0.4745, $r^2 = 0.95$). The datalogger would then trigger solenoid valves (2.5 cm, 24 VAC solenoid valves; Nelson Turf, Peoria, IL) to open for twenty seconds if the θ was below the treatment set point. When solenoid valves opened, plants were irrigated using pressure compensated dribble rings (internal diameter ≈ 13 cm; Dramm, Manitowoc, WI). The total number of irrigation events was recorded by the datalogger and later multiplied by the volume of water emitted during a single irrigation event (information obtained prior to each experiment) to determine the total volume of water applied to each plant over the entire investigation.

Supplemental lighting was provided by 600 watt high pressure sodium lights (PL2000, P.L. Light Systems Inc., Beamsville, ON) from 0800 $_{HR}$ to 2000 $_{HR}$. Light levels were monitored using a quantum sensor (Model QSO-S, Apogee Instruments, Inc., Logan, UT) connected to a datalogger (CR10X, Campbell Scientific, Logan, UT)

programmed to record instantaneous light levels ($\mu mol \cdot m^{-2} \cdot s^{-1}$) every five minutes throughout the entire investigation. Daily light integral (DLI, $mol \cdot m^{-2} \cdot d^{-1}$) was calculated using the mean of the instantaneous light levels in the following equation: ($\mu mol \cdot m^{-2} \cdot s^{-1}$ x 60 $sec \cdot min^{-1}$ x 60 $min \cdot hr^{-1}$ x 24 $hr \cdot day^{-1}$) ÷ 1,000,000 $\mu mol \cdot mol^{-1}$. Plants received a mean DLI of 22.0 $mol \cdot m^{-2} \cdot d^{-1}$.

Height of plants from the top of the substrate to the uppermost leaf and widest width were measured once weekly throughout the entire investigation. Floral stalks, and any leaves associated with them, were not included in height and width measurements. On the final day of each experiment, total leaf area was measured on one representative plant from each experimental unit using a leaf area meter (LI-3100A; LI-COR Biosciences, Lincoln, NE). Total number of leaves on all subsamples was counted. Shoot tissue was dried in a soil drying room and dry mass was later noted. Specific leaf area (SLA) was calculated by dividing the total leaf area by the shoot dry mass ($cm^2 \cdot g^{-1}$).

In each experimental unit one sensor was within a container. Measurements from this sensor were used to control irrigation in that container, and two neighboring containers. There were a total of three subsamples for each experimental unit. Independent measurements from a hand-held WET sensor (Delta T Devices, Cambridge, U.K.) were used to ensure that θ was maintained at the appropriate set point in containers without a sensor. The experimental design was a randomized complete block design with two blocks for each treatment.

2.3.2 Experiment 2: Light

The light investigation ran for 45 days starting on 19 May 2008. Plant material and initial cultural methods (i.e. transplanting, initial watering, and fertilizer application) for this study were obtained and conducted in the same manner described in the water study described above. The supplemental light described in the water experiment was also provided in the same manner above all plants in the light study.

Plants were grown at four different light levels (0, 30, 60, and 90% shaded). Shade was provided by square (0.6 × 0.6 × 0.6m) polyvinyl (PVC) pipe structures covered with a single, double, or triple layer of commercial 30% shadecloth (K-Pro Supply; Sarasota, FL), respectively. Zero percent shade treatment plants were simply grown on the greenhouse benches without a PVC structure over them. An experimental unit consisted of one shade treatment over four plants. Light levels were monitored under each experimental unit using a quantum sensor set up in the same manner as those used in the water deficit experiment. Daily light integrals resulting from the shade treatments were 21.8, 14.9, 10.8, and 7.5 $mol \cdot m^{-2} \cdot d^{-1}$ for the structures covered with 0, 30, 60, and 90% shade cloth, respectively. θ was maintained at 0.35 $L \cdot L^{-1}$ for plants grown under all DLIs using the automated irrigation system described above. Independent measures of θ using the handheld sensor were conducted in the same manner as detailed in the earlier methodology.

All weekly and final measures were noted using the same methods described for the water study. Experimental units were set up in a randomized complete block design with four blocks.

All data were analyzed using regression analysis and Fisher's LSD means separation in Statistical Analysis Systems (version 9.1; SAS Institute, Cary, NC). *P*-values less than or equal to 0.05 were considered statistically significant.

2.4 Results and Discussion

2.4.1 Substrate water content and volume of water applied

Once the containers dried to their respective treatment levels, θ was maintained close to all set points throughout the remainder of both investigations (Fig. 2.1a and 2.1b). The total volume of water applied throughout the irrigation experiment increased linearly with increasing θ set point (Fig. 2.1c). Applied water ranged from 2.6L (± 0.10) in substrates maintained at a θ of 0.15 $L \cdot L^{-1}$ to 5.0L (± 0.08) in substrates maintained at 0.5 $L \cdot L^{-1}$. Irrigation totals increased in a quadratic manner in relation to DLI, with values ranging from 3.6L (± 0.10) in the lowest DLI to 5.7 in the highest DLI (± 0.55) (Fig. 2.1d). The increase in volume of water applied was likely due to increases in evapotranspiration under higher light levels (include general light/water citation). Others have also reported a correlation between DLI and irrigation frequency using an automated system based on θ (van Iersel et al., 2010).

2.4.2 Experiment 1: Water

Total leaf area was positively correlated with θ (Fig. 2.2b). Leaf area of plants growing in the highest set point was approximately double (1678 ± 415 cm^2) that observed in the lowest set point (804 ± 2 cm^2). A change in the yield threshold of the cell wall has been noted to be the primary factor influencing cell expansion when soil water

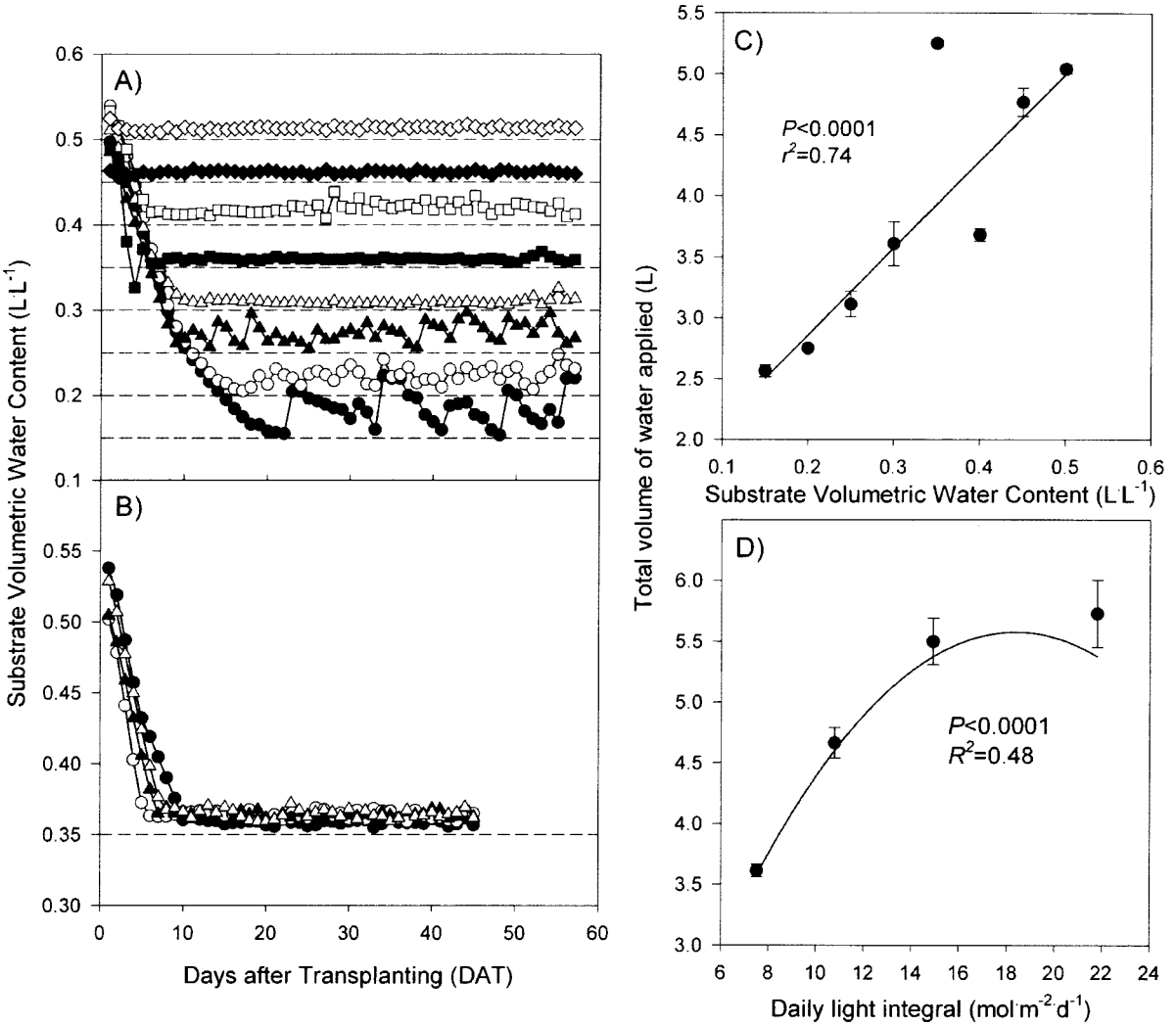

Figure. 2.1. Substrate volumetric water content over time during the water study (A) and the light study (B) and total volume of water applied over the entire course of the water study (C) and the light study (D).

status is limiting (Lambers et al., 2008; van Volkenburgh, 1999). Final leaf count did not differ among treatments, giving more evidence that cell expansion was the primary factor responsible for leaf area differences (Fig. 2.2c). Reduced leaf area in response to lower water availability has been reported in a number of studies (Burnett et al., 2005; Niu et al., 2006; Sánchez -Blanco et al., 2009; Starman and Lombardini, 2006; Zollinger et al., 2006).

Shoot dry weight was also positively correlated with θ set point (Fig. 2.2a). Plants grown in substrates irrigated at the lowest set point (0.15 $L \cdot L^{-1}$) weighed 7.63 ± 0.58g, while plants grown in substrates irrigated at the highest set point (0.5 $L \cdot L^{-1}$) were 9.75 ± 0.62g. Increases in leaf area were likely a dominant factor in influencing shoot dry weight (Jones, 1992). *Pelargonium x hortorum* L. (bedding geranium) and *Plumbago auriculata* Lam. (plumbago) are examples of other ornamental crops that have smaller dry weights and leaf areas when exposed to water deficits (Niu, et al., 2006; Sánchez - Blanco, 2009).

Weekly measures of height and width did not differ among θ set points, nor did final measures of height and width (data not shown). At the end of the experiment, height and width of heuchera averaged 13.3 ± 0.21 and 28.0 ± 0.49 cm, respectively. Some plants change leaf orientation to avoid sunlight (paraheliotropic) in response to drought (Smith et al., 2004; Taiz and Zeiger, 2006). Since heuchera has basal foliage, changes in leaf orientation would greatly impact plant height and width.

SLA was also not influenced by the irrigation regime. Water stress can have different impacts on SLA depending on the age of the tissue being examined (Marron et al., 2003). When exposed to a period of drought, SLA was reduced in relatively young,

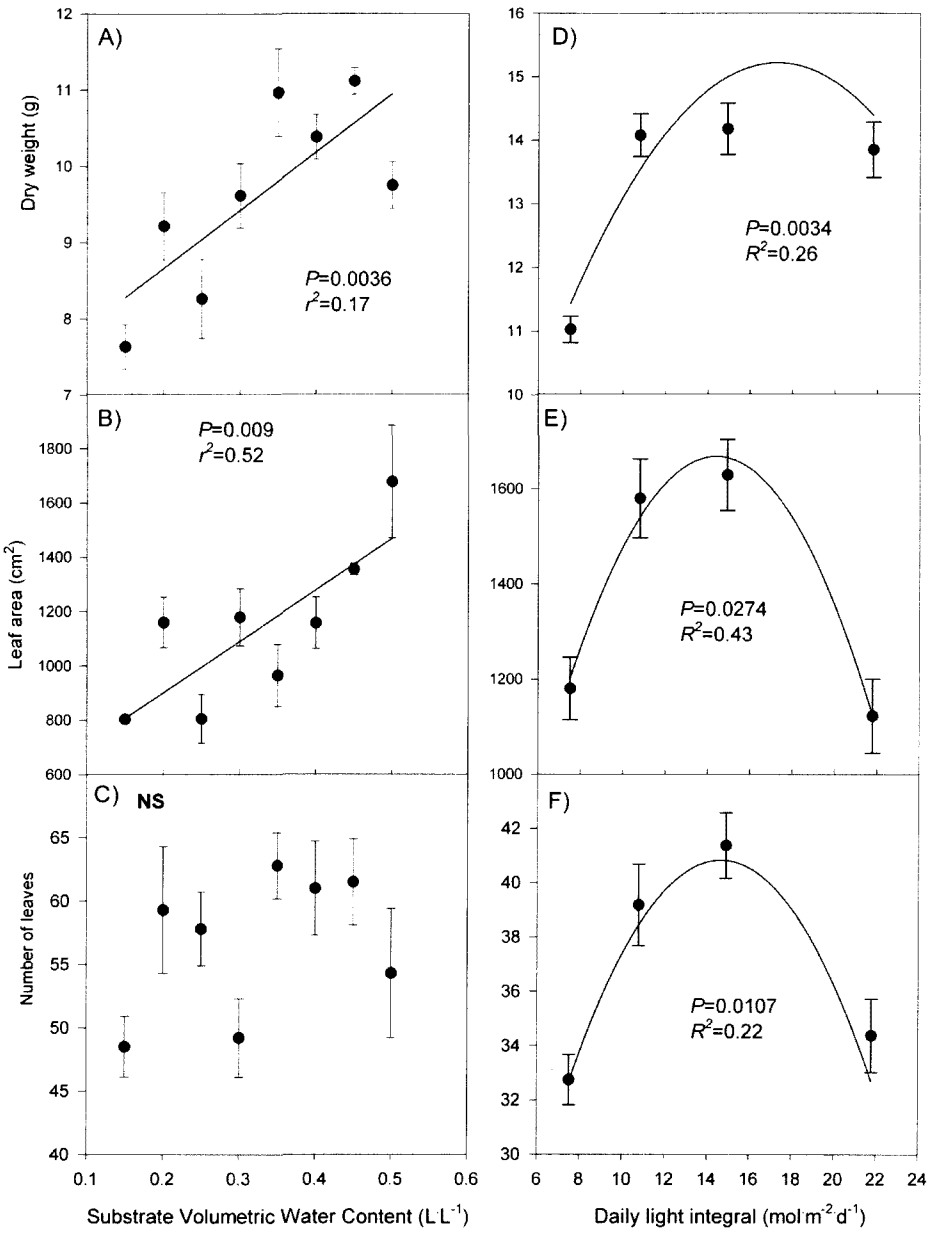

Figure 2.2. The influence of substrate volumetric water content (A-C) and daily light integral (DLI) (D-F) on shoot dry weight (A and D), total leaf area (B and E), and total number of leaves (C and F) of *Heuchera americana* 'Dale's Strain'.

yet mature, poplar (*Populus* x *canadensis* (Moench)) leaves while increases in SLA were observed in older foliage on the same plant. This phenomenon is likely the result of resource allocation patterns favoring younger leaves. By increasing soluble sugars in new foliage, plants are better able to maintain leaf water status in this tissue during limiting conditions (Marron et al., 2003). SLA was assessed in the current investigation using whole plant measures of leaf area (cm^2) and shoot dry weight (g). Therefore, it is possible that θ could have impacted the SLA of heuchera in a similar fashion, but was undetectable from the mode of assessment used here.

2.4.3 Experiment 2: Light

Dry weight was significantly reduced in the lowest light treatment, but did not differ among the three higher DLIs, indicating that heuchera encountered saturating light levels somewhere around 11 $mol \cdot m^{-2} \cdot d^{-1}$ (Fig. 2.2d). Mean dry weights for plants grown under 7.5, 10.8, 14.9, and 21.8 $mol \cdot m^{-2} \cdot d^{-1}$ were 11.0, 14.1, 14.2, and 13.9g, respectively. Outdoor DLIs throughout the U.S. during spring and early summer production periods range somewhere around 15 to 35 $mol \cdot m^{-2} \cdot d^{-1}$ in the Northeast and 55 to 60 $mol \cdot m^{-2} \cdot d^{-1}$ in the Southwest (Korcynski et al., 2002). DLIs inside a greenhouse may be reduced up to 50%, depending on the glazing and structure type (Fisher and Runkle, 2004). Considering dry weight alone, supplemental lighting is not necessary for heuchera throughout most of the U.S. during spring and early summer production periods.

Leaf area trended in a quadratic manner with increasing DLI (Fig. 2.2e). The largest leaf areas were measured in plants grown under DLIs of 10.8 and 14.9 $mol \cdot m^{-2} \cdot d^{-1}$ compared to those at 21.8 and 7.5 $mol \cdot m^{-2} \cdot d^{-1}$. Reduced total leaf area was likely a result

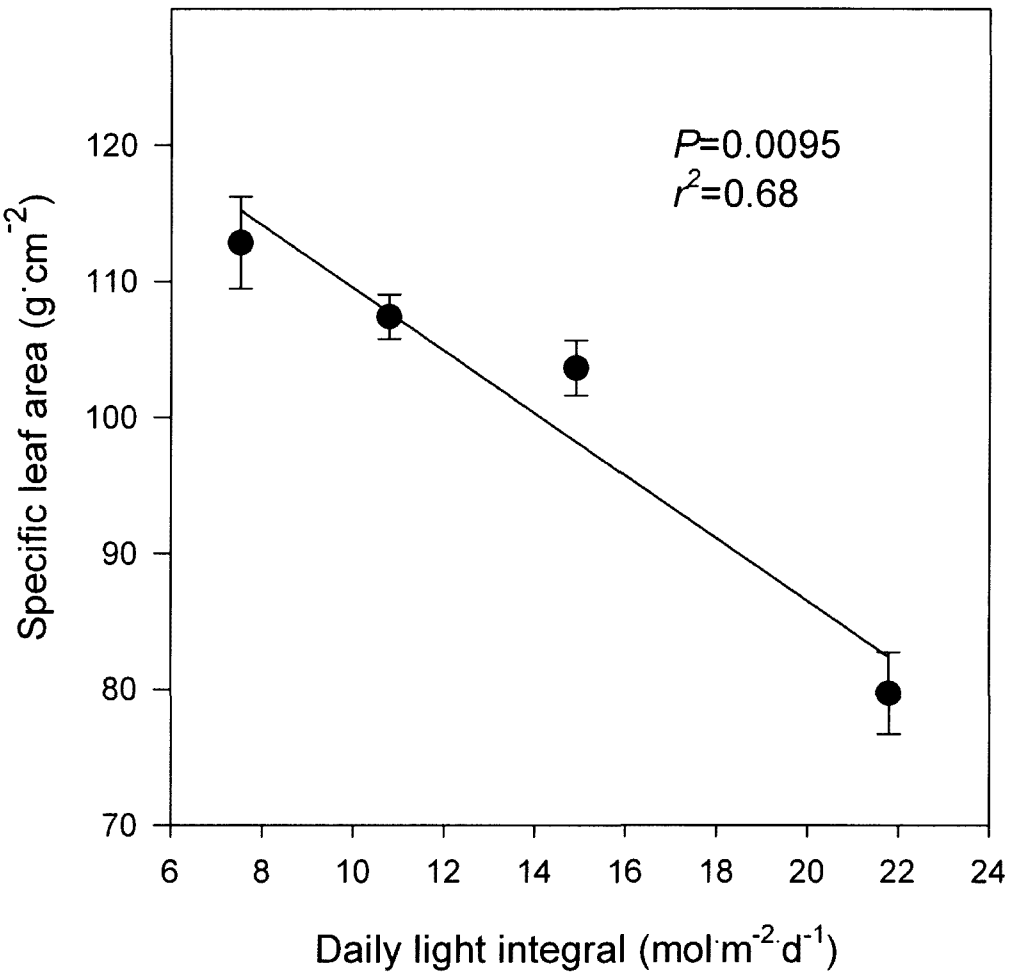

Figure 2.3. The effect of daily light integral on specific leaf area of *Heuchera americana* 'Dale's Strain'.

of lower relative leaf counts in the highest DLI. Leaf count increased quadratically with DLI resulting in a mean of 32.8, 39.2, 41.4 and 34.4 leaves on plants growing in 7.5, 10.8, 14.9, and 21.8 $mol \cdot m^{-2} \cdot d^{-1}$, respectively (Fig. 2.2e). Other crops reported to yield higher leaf counts with increasing DLI include *Cyclamen persicum* Mill. 'Metis Scarlet Red' (cyclamen) and *Adiantum raddianum* C. Presl 'Fritz Luth' (maidenhair fern) (Oh et al., 2009; Yeh and Wang, 2000).

Lower leaf areas noted at the highest DLI did not correspond with a similar decrease in dry weight. Instead, leaves exposed to 21.8 $mol \cdot m^{-2} \cdot d^{-1}$ had a lower specific leaf area ($cm^2 \cdot g^{-1}$) compared to the other three DLIs (Fig. 2.3). SLA was negatively correlated with DLI throughout the range of light levels tested. This change in leaf structure has been previously reported in *Heuchera americana* (Skillman et al., 1996) as well as in other species including ageratum (*Ageratum houstonianum* L.), begonia (*Begonia* x*semperflorens-cultorum* L.), impatiens (*Impatiens wallerana* L.), marigold (*Tagetes erecta*), petunia (*Petunia* × *hybrida* Juss.), salvia (*Salvia coccinea* L.), vinca (*Catharanthus roseus* L.), and zinnia (*Zinnia elegans* L.) (Faust et al., 2005). In thinner, shade-adapted leaves, light travels a shorter distance to the chloroplasts in the palisade parenchyma cells (Evans, 1999). Lower leaf area in the higher light treatments may have reduced the total amount of water loss from transpiration, supporting the notion that reduced leaf area can be a water management strategy in plants exposed to high light (Yeh and Wang, 2000). This is supported by the reduced demand for water per unit of daily light integral observed in the higher light treatments without a corresponding change in biomass (Fig. 2.1d and Fig. 2.2d).

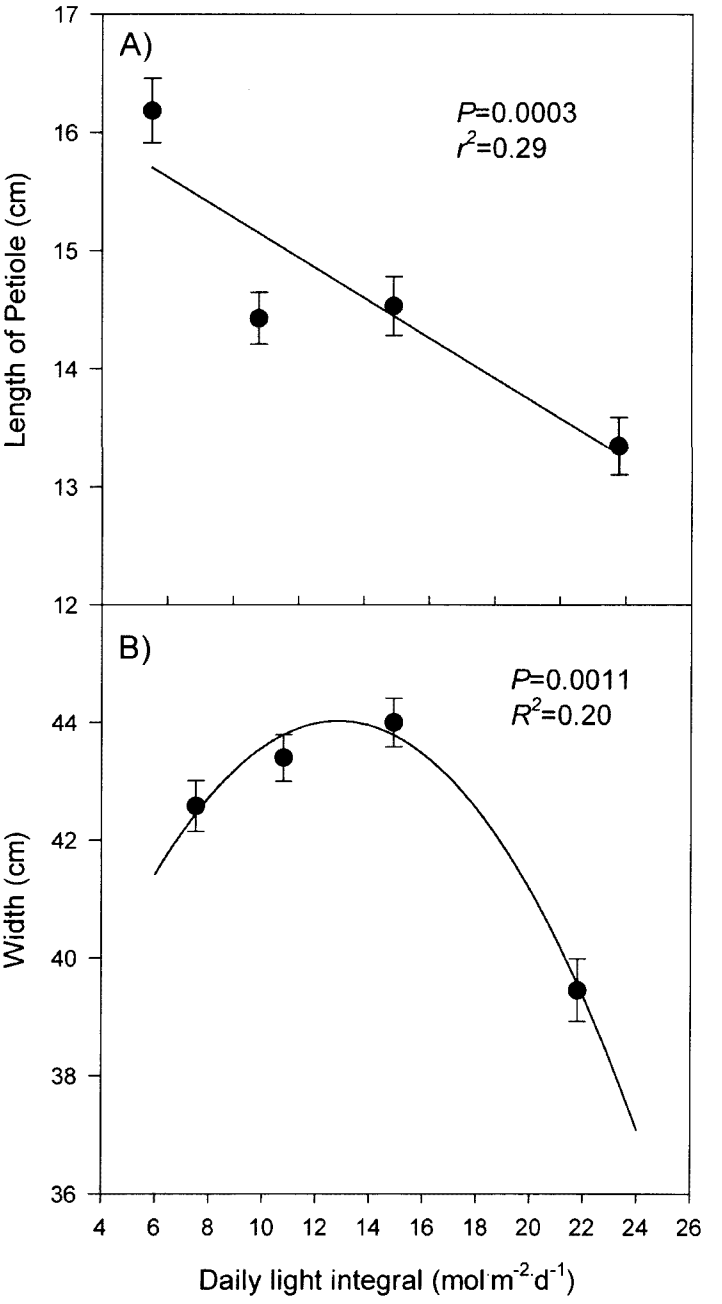

Figure 2.4. Petiole length of uppermost fully expanded leaf (A) and maximum crown width (B) of *Heuchera americana* 'Dale's Strain' grown under four daily light integrals.

Altering leaf orientation may also increase or decrease plant exposure to irradiance. Many plants native to understory habitats, such as heuchera, are capable of minimizing mutual shading in low light conditions. Shade adapted species, such as the herbaceous understory plant *Adenocaulon bicolor* Hook. (trail plant) are known to effectively manage leaf arrangement, petiole length, leaf angle, and leaf size in a manner that results in an optimal design for light capture (Pearcy and Yang, 1998). In lower light levels, petiole length of the uppermost fully expanded leaf increased, allowing plants to reduce the competition for light (Fig. 2.4a). Maximum crown width increased with decreasing DLI (Fig. 2.4b). For heuchera, width is a function of both petiole length and leaf area. Differences in crown width were not significant until the end of the experiment. Height was not influenced in early or later stages of the investigation (data not shown).

2.5 Conclusions

Substrate water content and daily light integral both have a significant impact on the growth and morphology of heuchera. Supplemental lighting is considered a useful investment for heuchera production in settings where light levels are below 11 $mol \cdot m^{-2} \cdot d^{-1}$ and shading materials should be considered if light levels are beyond 15 $mol \cdot m^{-2} \cdot d^{-1}$. Growers would benefit from producing heuchera at θ somewhere between 0.35 and 0.5 $L \cdot L^{-1}$, as higher θ increased both leaf area and biomass production. Using a capacitance sensor automated irrigation system to irrigate heuchera would conserve water. Plants irrigated using this system needed no more than 5L of water, even when they were irrigated at the highest water content (0.5 $L \cdot L^{-1}$).

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CHAPTER 3:

INFLUENCE OF SUBSTRATE WATER CONTENT AND DAILY LIGHT INTEGRAL ON PHOTOSYNTHESIS, FLUORESCENCE, AND WATER USE EFFICIENCY OF *HEUCHERA AMERICANA*

3.1 Abstract

A capacitance sensor automated irrigation system was used to accurately maintain substrate volumetric water content (θ) during two experiments examining the effects of light and water on physiology of *Heuchera americana* L. 'Dale's Strain' (heuchera). In experiment 1, plants were grown in substrates maintained at one of eight θ set points (0.15, 0.20, 0.25, 0.30, 0.35, 0.40, 0.45 or 0.50 $L \cdot L^{-1}$). In experiment 2, heuchera were grown under one of four daily light integrals (DLI) (7.5, 10.8, 14.9, 21.8 $mol \cdot m^{-2} \cdot d^{-1}$) while maintaining θ at 0.35 $L \cdot L^{-1}$. Carbon dioxide response curves were developed in both experiments and a light response curve was developed in the light experiment. A unique comparison of three different measures of water use efficiency (WUE) was also assessed in both experiments. Irrigation-based WUE: shoot dry weight/volume of water applied (WUE_I) was calculated using precise irrigation data obtained from the capacitance sensor automated irrigation system. Two physiological metrics of WUE: net photosynthetic rate (A_N) per unit of water lost via transpiration (E) ($A_N \cdot E^{-1}$) (WUE_E) and A_N per unit of water lost via stomatal conductance (g_s) ($A_N \cdot g_s^{-1}$) (WUE_{gs}) were calculated from gas exchange measurements.

In experiment 1, plants maintained similar leaf water, osmotic, and turgor potential and net photosynthesis among all θ treatments. For plants grown in substrates maintained at all θ set points, the relative concentration of carbon dioxide (CO_2) inside

the leaf (C_i) to ambient CO_2 concentrations (C_a) (C_i/C_a) was highly correlated with g_s and was not correlated with A_N. In experiment 2, shade tolerant heuchera survived all of the light levels provided, but plants did not increase net photosynthesis to utilize the additional light received in the higher light treatments. Instantaneous gas exchange measures revealed a linear decline in both g_s and E with increasing light levels, but no changes were observed in A_N. C_i/C_a was positively correlated with both g_s and A_N, suggesting that C_i was influenced by both the rate of CO_2 diffusion into the leaf and the rate of CO_2 consumption within the leaf. WUE_I, was negatively correlated with θ (i.e. more shoot dry matter was produced per unit of water applied with decreasing θ set point). Meanwhile, WUE_E and WUE_{gs} were not influenced by θ. In the light study, WUE_I, decreased with increasing light. However, both physiological measures of WUE indicated an increase in water use efficiency at higher light levels. Although all three measures of WUE are acceptable means of reporting plant water use, this research supports the notion that it is important be aware that each can yield seemingly contradictory results due to their inherently different meanings. Therefore, care should be taken to choose the WUE measure that will fulfill the specific research goals of the study being conducted.

3.2 Introduction

Water and light have been the focus of countless studies assessing plant response to abiotic stress. Both factors have been investigated independently as well as in combination with one another. The methods used to apply light and water stress can vary dramatically from study to study. Zollinger et al. (2006) subjected plants to water deficit

by watering them once every 2 or 4 weeks for a full season. Eakes et al. (1991) allowed plants to dry down to visible wilt before rehydration. Meanwhile, several others drought stressed plants by refraining from watering until containers reached a certain target weight (Niu et al., 2006; Sánchez-Blanco et al., 2009; Starman and Lombardini, 2006). These methods can be time consuming and may result in greater fluctuations in the actual substrate volumetric water content (θ) compared to other methods of regulated deficit irrigation. Further, studies that rely on container weight to indication soil water status may not account for changes in root and/or shoot mass that may differ from container to container, which could result in a significant source of experimental error. An alternative to these methods is to initiate irrigation events according to θ measurements from sensors (Burnett et al., 2008; Nemali and van Iersel, 2008). The automated irrigation system described in Nemali and van Iersel (2006) uses capacitance sensors permanently located in the substrate to monitor θ. Measurements are relayed to a computer which triggers a solenoid valve to open if θ is too low. This system accurately maintains θ throughout the duration of an experiment, regardless of differences in environmental conditions or plant size (Nemali and van Iersel, 2006; Burnett et al., 2008).

Capacitance sensor automated irrigation systems provide an accurate way to maintain θ for studies examining physiological effects of drought stress. Further, using this type of irrigation system in light studies minimizes the potential for error from differences in θ. If an irrigation system is not responsive to changes in soil water status due to increased evaporative demand, water stress can occur in plants exposed to high light or, conversely, plants growing in low light may experience periods of excessive water supply (Burnett and van Iersel, 2010). Plant response to the combined forces of

light and water are far from being fully understood and therefore should be avoided in studies in which the research goal is to assess light as the only variable. Some research suggests that plants exposed to shade have a tendency to allocate more resources towards the production of light capturing organs than moisture capturing organs thus leaving them more sensitive to drought stress (Valladares and Pearcy, 2002). On the other hand, several studies have observed that shading lessens the impact of water stress on plants (Holmgren, 2000; Prider and Facelli, 2004). Some researchers have even observed evidence that the effects of shade and drought are independent (Quero et al., 2006). Because the combined influence of water and light are not well understood, a moisture sensor automated irrigation system such as the one described earlier, would be an effective tool to eliminate potential sources of error associated with water stress in light studies.

An additional benefit to using a capacitance sensor automated system is that it can monitor the precise amount of water applied throughout an entire growing cycle. Irrigation data, such as this, can provide key information regarding the efficiency in which water is used to produce a crop (i.e. water use efficiency (WUE)). The term WUE can be applied on a number different scales ranging from field-level production (i.e. seasonal grain yield per volume of water applied) to leaf-level gas exchange (i.e. net CO_2 assimilation for a given amount of evaporative loss) (Sinclair et al., 1984). Irrigation based measures of WUE using an automated system that is proven to not overwater can be an effective means of assessing whether varying environmental variables such as water and light can allow growers to obtain a greater yield for the amount of water applied. Meanwhile, instantaneous gas exchange measures of WUE can provide a picture

of how well a plant is managing internal water resources in response to environmental variations in water and light. These two types of measures can both provide a valid assessment of WUE, even though they may yield very different results due to their inherently different meanings (Sinclair et al., 1984).

Plants respond to light and water in a number of ways beyond WUE. Responses vary from species to species (Seemann et al., 1987; Zollinger et al., 2006) and even among cultivars (Miller et al., 2001; Niu et al., 2008). For example, when exposed to high light, the sun adapted plant *Phaseolus vulgaris* L. (common bean) has a greater capacity to adjust the allocation of nitrogen resources towards greater Rubsico content compared to the shade adapted plant *Alocasia macrorrhizos* (L.) G. Don (giant tarro). Meanwhile, when both species are exposed to shade, the giant taro is more likely to allocate nitrogen resources towards higher chlorophyll content compared to the common bean (Seemann et al., 1987). Miller (2001) reported that, under the same light conditions, two cultivars of the *Angelonia angustifolia* Benth. had different quantum yields and light compensation points (LCP), suggesting a reason for one having a faster growth habit than the other. Zollinger et al. (2006) reported that *Echinacea purpurea* (L.) Moench (purple cone flower) responded to less frequent irrigation with reduced stomatal conductance (g_s) and lower rates of net photosynthesis (A_N); whereas *Penstemon barbatus* Roth var. *praecox nanus rondo* (penstemon) was able to maintain similar rates of g_s and A_N throughout all of the irrigation treatments.

Response to differing light and water availability also depends on the degree and intensity of the stress imposed as well as the conditions that the plant acclimated to prior to the experiment (Kramer and Boyer, 1995; Pospíšilová and Dodd, 2005). Many species

previously exposed to drought have a higher relative root to shoot mass that provides them with greater water capturing ability during subsequent water stress (Franco et al., 2008). g_s may not fully recover after periods of severe stress, and combined with reduced leaf areas traditionally observed with water stress, can both lower whole plant water loss; which also enhance the chances of plant survival in future deficit conditions (Franco et al., 2006). Plants exposed to sustained or periodic water stress may also have stomata that are more sensitive to abscisic acid (ABA) which is the primary hormone responsible for stomatal closure during water stress (Pospíšilová and Dodd, 2005).

Heuchera americana L. (heuchera) is an evergreen herbaceous perennial native to deciduous understory habitats ranging from Ontario to Louisiana and Nebraska to Connecticut (Skillman and Osmond, 1998; USDA, 2009). In the winter, under an open canopy, native heuchera are often exposed to cumulative daily light integrals (DLI) 3-10 times that observed in the summer. Despite the colder temperatures, photosynthetic capacity increases during the winter high-light period without any sign of photoinhibition (Skillman et al., 1996). However, summer fluorescence measures taken on heuchera grown in an open field setting indicated damage to PSII (Skillman and Osmond, 1998).

Over 350 ornamental cultivars have been developed from the genus *Heuchera,* with more being introduced every year (Heims and Ware, 2008). To our knowledge, A_N and estimates of photosynthetic capacity (other than fluorescence) have not been determined for heuchera growing under light levels higher than those observed in its native habitat. These estimations would be a helpful indicator of appropriate light levels for growing this crop in a greenhouse for commercial sales.

If capacitance sensor automated irrigation systems based on θ are to be implemented in production settings, it would be of great use to determine the θ requirements of the crops being grown. There is little more than anecdotal information regarding the specific water requirements of heuchera (Cullina, 2000; Heims and Ware, 2005). Therefore, the objectives of this investigation are: 1) to explore whether heuchera has the physiological capacity to acclimate to light levels higher than those experienced in its native habitat, 2) to determine whether deficit irrigation has an impact on stomatal and non-stomatal limitations to photosynthesis, and 3) to present a comparison of how three different measures of WUE respond to differing water and light availability.

3.3 Materials and Methods

3.3.1 Experiment 1: Water

The water study began on 5 May 2008 and continued for 56 days. Pre-vernalized *H. americana* 'Dale's Strain' young plants were obtained from a commercial nursery (Bluestone Perennials, Madison, OH). Plugs were transplanted into 3.8 L containers using a commercial substrate (Fafard 2P, 60% peat:40% perlite (v/v), Conrad Fafard Corp., Agawam, MA). All containers were irrigated to container capacity immediately after planting and were subsequently watered with a continuous liquid feed of 200 $mg \cdot L^{-1}$ N solution (Peters EXCEL 15N-2.2P-12.45K Cal-Mag, The Scotts Co., Marysville, OH). Beginning 10 June, 2008, the fertilizer solution was changed so that 100 $mg \cdot L^{-1}$ N was provided by the previously mentioned commercial fertilizer and another 100 $mg \cdot L^{-1}$ N was applied in the form of calcium nitrate ($CaNO_3$).

Plants were irrigated using a capacitance sensor automated irrigation system (Nemali and van Iersel, 2006) which maintained a constant substrate volumetric water content (θ) at one of eight θ set points (0.15, 0.2, 0.25, 0.3, 0.35, 0.4, 0.45 or 0.5 $L \cdot L^{-1}$). In this system, capacitance sensors (EC-5; $\approx$ 5cm x 2cm, Decagon Devices, Pullman, WA) were set to measure the voltage of the substrate every five minutes. Sensors relayed the voltage to a CR-10X datalogger (Campbell Scientific, Logan, UT) where the voltage measurement was used to calculate θ using a substrate specific calibration equation (θ = voltage $\times$ 1.7647 – 0.4745, $r^2 = 0.95$). The datalogger would then trigger solenoid valves (2.5 cm, 24 VAC solenoid valves; Nelson Turf, Peoria, IL) to open for twenty seconds if θ was below the treatment set point. When solenoid valves opened, plants were irrigated using pressure compensated dribble rings (internal diameter $\approx$ 13 cm; Dramm, Manitowoc, WI). The total number of irrigation events was recorded by the datalogger and later multiplied by the volume of water emitted during a single irrigation event (information obtained prior to each experiment) to determine the total volume of water applied to each plant over the entire investigation.

Supplemental lighting was provided by 600 watt high pressure sodium lights (PL2000, P.L. Light Systems Inc., Beamsville, ON) from 0800 $_{HR}$ to 2000 $_{HR}$. Light levels were monitored using quantum sensors (Model QSO-S, Apogee Instruments, Inc., Logan, UT) connected to a datalogger (CR10X, Campbell Scientific, Logan, UT) programmed to record instantaneous light levels ($\mu mol \cdot m^{-2} \cdot s^{-1}$) every five minutes throughout the entire investigation. Daily light integral (DLI, $mol \cdot m^{-2} \cdot d^{-1}$) was calculated using the mean of the instantaneous light levels in the following equation: ($\mu mol \cdot m^{-2} \cdot s^{-1}$ x 60 $sec \cdot min^{-1}$ x 60 $min \cdot hr^{-1}$ x 24 $hr \cdot day^{-1}$) $\div$ 1,000,000 $\mu mol \cdot mol^{-1}$.

Midday leaf water (Ψ_W), osmotic (Ψ_S), and turgor (Ψ_P) potential were obtained during the final week of the water deficit experiment using leaf cutter thermocouple psycrometers (J.R.D Merrill Specialty Equipment, Logan, UT). Samples were obtained between 1200 $_{HR}$ and 1300 $_{HR}$ from the uppermost fully expanded leaf of plants grown in the containers that held the capacitance sensors. Psycrometer chambers containing leaf samples were initially placed in a 25°C water bath for 4h before taking readings of Ψ_W. Chambers were then placed in a freezer overnight in order to disrupt cell membranes, thus eliminating Ψ_P. The following day, the chambers were once again placed in a 25°C water bath for 4h and samples were subsequently measured to obtain Ψ_S. Ψ_P was calculated using the following equation: $\Psi_W - \Psi_S = \Psi_P$.

Leaf gas exchange was evaluated during the final week of the study using a portable open-flow photosynthesis system (LI-6400, LI-COR) equipped with a red/blue LED light source. Unless otherwise noted, all measures were performed on the uppermost fully expanded leaves of a representative plant from each experimental unit. Linear and non-linear estimates of photosynthetic parameters were obtained using SYSTAT (version 12, SYSTAT Software, Inc. Evanston, IL).

Photosynthetic carbon dioxide response (A_N-Ci) curves were developed for one block of plants by exposing leaves to the following carbon dioxide concentrations: 400, 300, 250, 200, 150, 100, 50, 40, 350, 450, 600, 700, 800, 900, 1000, 1200 $mL \cdot L^{-1}$ allowing for ample time for leaf CO_2 uptake (A_N) to reach steady state within the leaf chamber. Photosynthetic photon flux density (PPFD) was maintained at saturating levels (400-480 $mol \cdot m^{-2} \cdot s^{-1}$) (Skillman et al., 1998), mean leaf temperature was 21.5°C and relative humidity within the chamber was manually maintained at approximately 65-70%.

Respiration and the maximum carboxylation rate of rubisco (Vc_{max}) were estimated from a linear regression line fitted to the initial part of the A_N-C_i response curve (C_i <400 $\mu mol \cdot m^{-2} \cdot s^{-1}$). Respiration ($R_d$) was estimated to be the point where the regression line crossed the Y-axis and Vc_{max} was estimated using the following model: $\mathbf{A_N = C_i * Vc_{max} - R_d}$ where C_i is the concentration of CO_2 within the leaf and A_N represents the net rate of photosynthesis (Long and Bernacchi, 2003).

J_{max}, the light saturated electron transport rate driving the regeneration of ribulose-1,5-bisphosphate (RuBP), was estimated using the latter part of the A_N-C_i response curve (C_i=400-900 $\mu mol \cdot m^{-2} \cdot s^{-1}$) with the following model: $\mathbf{A_N = g' * J_{max} - R_d}$ where g' is obtained from the following calculation: $g' = \frac{Ci - \Gamma^*}{4.5 * Ci + 10.5\,\Gamma^*}$. Γ^* represents the photosynthetic compensation point at the chloroplast, which was estimated to be 37 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Bernacchi et al., 2002; Long and Bernacchi, 2003).

Apparent quantum efficiency of the photosystem II (Fv/Fm) was determined using a LI-COR LI-6400-40 leaf chamber fluorometer integrated with the LI-6400 portable photosynthesis system.

Instantaneous gas exchange measures of A_N, g_s, and E were used to calculate two metrics of water use efficiency, A_N/g_s and A_N/E (WUE_{gs} and WUE_E, respectively). Values were obtained at CO_2 levels of 400 $mL \cdot L^{-1}$ and saturating PPFD. Water use efficiency (g/L) was also calculated by dividing the shoot dry weight by the total water applied (number of irrigation events * volume of water applied during each irrigation event).

In each experimental unit one sensor was within a container. Measurements from this sensor were used to control irrigation in that container, and two neighboring

containers. There were a total of three subsamples for each experimental unit. Independent measurements from a hand-held WET sensor (Delta T Devices, Cambridge, U.K.) were used to ensure that θ was maintained at the appropriate set point in containers without a sensor. The experimental design was a randomized complete block design with two blocks for each treatment.

3.3.2 Experiment 2: Light

The light investigation ran for 45 days beginning 19 May 2008. Plant material and initial cultural methods (i.e. transplanting, initial watering, and fertilizer application) for this study were conducted in the same manner as they were in the water deficit experiment described above. The supplemental lighting mentioned in the water deficit study was also used to enhance light levels above all treatments during the light investigation.

Plants were grown at four different light levels (0, 30, 60, and 90%). Shade was provided by square (0.6 × 0.6 × 0.6m) polyvinyl (PVC) pipe structures covered with a single, double, or triple layer of commercial 30% shadecloth (K-Pro Supply; Sarasota, FL), respectively. Zero percent shade treatment plants were simply grown on the greenhouse benches without a PVC structure over them. An experimental unit consisted of one shade treatment over four plants. Light levels were monitored under each experimental unit using a quantum sensor set up in the same manner as those used in the water deficit experiment. Daily light integrals resulting from the shade treatments were 21.8, 14.9, 10.8, and 7.5 $mol \cdot m^{-2} \cdot d^{-1}$ for the structures covered with 0, 30, 60, and 90% shade cloth, respectively. θ was maintained at 0.35 $L \cdot L^{-1}$ for plants grown under all DLIs

using the automated irrigation system described above. Independent measures of θ using the handheld sensor were conducted in this study as well. Type T thermocouples were connected to the datalogger which was programmed to continuously monitor temperature under each experimental unit. A temperature gradient was observed among blocks due to varying distances from the evaporative cooling system in the greenhouse, but differences were not observed among treatments.

Instantaneous measures of A_N, g_s, and E were obtained on one representative plant in each experimental unit in the same manner described above. A_N-Ci curves were developed for a representative plant in each experimental unit of the high light and low light treatments only. Methods for gas exchange measures and for calculating photosynthetic parameter estimates are the same as those in the water experiment.

Light response (A_N-Q) curves were developed using one representative plant from each experimental unit. Leaves were exposed to the following incremental levels of photosynthetically active radiation (PAR): 2000, 1500, 1000, 500, 200, 100, 50, 20, and 0 $\mu mol \cdot m^{-2} \cdot s^{-1}$ providing ample time for photosynthesis to approach equilibrium. Carbon dioxide concentration within the leaf chamber was kept at 400 $mL \cdot L^{-1}$, mean leaf temperature was 23.4 °C, and relative humidity remained approximately 65-70%.

Dark respiration (R_d) was estimated using linear regression from the initial part of the light response curve where the PPFD was below 90 $mol \cdot m^{-2} \cdot s^{-1}$. Quantum efficiency (*QE*) and maximum rate of A_N (A_{max}) were estimated by fitting data to Prioul and Chartier's model function (1977):

$$A_N = \frac{QE * PPFD + Amax - \sqrt{(QE * PPFD - Amax)^2 - 4 * QE * PPFD * k * Amax}}{2k} - R_{day}$$

The light compensation point (LCP) was calculated as the point where the linear portion of the light response curve crosses the x axis (where y=0) using values determined for respiration (y intercept) and quantum efficiency (slope) in the slope intercept equation: $0 = QE^{*}LCP + R_{day}$.

Fluorescence, total amount of water applied, and all three measures of water use efficiency were measured using the techniques explained in the water deficit methodology.

A handheld chlorophyll meter (Minolta SPAD 502, Spectrum Technologies, Inc., Plainfield, IL) was used to non-destructively evaluate relative chlorophyll concentration in plants from the light investigation. This measurement was taken twice, 31 days after transplanting (DAT) and 43 DAT, on three different portions of the uppermost fully expanded leaf. These three measurements were averaged to obtain a more uniform measurement. Heuchera foliage is basal, therefore the uppermost fully expanded leaf was considered to be the highest held fully expanded leaf located nearest to the center of the crown. Care was taken to measure the area between leaf veins, as the vein tissue was darker green or purple compared to the rest of the leaf tissue.

Experimental units were set up in a randomized complete block design with four blocks. All data were analyzed using regression analysis and Fisher's LSD means separation in Statistical Analysis Systems (version 9.1; SAS Institute, Cary, NC). *P*-values less than or equal to 0.05 were considered statistically significant.

3.4 Results and Discussion

3.4.1 Substrate volumetric water content

After substrates dried down to their respective θ set points, the irrigation system maintained θ close to set points throughout the duration of both experiments (Fig. 3.1). Independent measurements of θ taken using a WET sensor were correlated to those taken with the in-situ EC-5 sensors ($P<0.0001$; $r^2=0.49$) in experiments 1 and 2. This confirmed that EC-5 sensors accurately maintained constant θ in both studies. Greater fluctuations observed in the three lowest set points were likely due to low hydraulic conductivity of peat-based substrates at low θ (Nemali and van Iersel, 2006). Similar trends have been observed in other studies (Burnett and van Iersel, 2008, Nemali and van Iersel, 2008).

3.4.2 Experiment 1: Water

Final measures of midday Ψ_W, Ψ_S and Ψ_P values were not correlated with θ (respective mean and standard errors: -1.55 ± 0.11, -1.95 ± 0.09, 0.47 ± 0.05 MPa). *Salvia splendens* F. Sellow. ex Roem & Shult.(annual salvia), *Catharanthus roseues* (L.) G. Don. (vinca), *Petunia x hybrida* Hort ex. Vilm. (petunia) and *Impatiens walleriana* Hook F. (impatiens) have also been reported to have little difference in Ψ_W between plants grown at θ set points of 0.15 $L \cdot L^{-1}$ or higher (Nemali and van Iersel, 2008; van Iersel, unpublished data). Burnett et al. (2005) reported that increasing substrate-applied concentrations of polyethylene glycol 8000, which reduces substrate Ψ_S, reduced foliar Ψ_W and Ψ_S of annual salvia 21 days after beginning the treatment, but differences were less pronounced at day 35 and day 56. Similar adjustments in Ψ_W and Ψ_S over time have

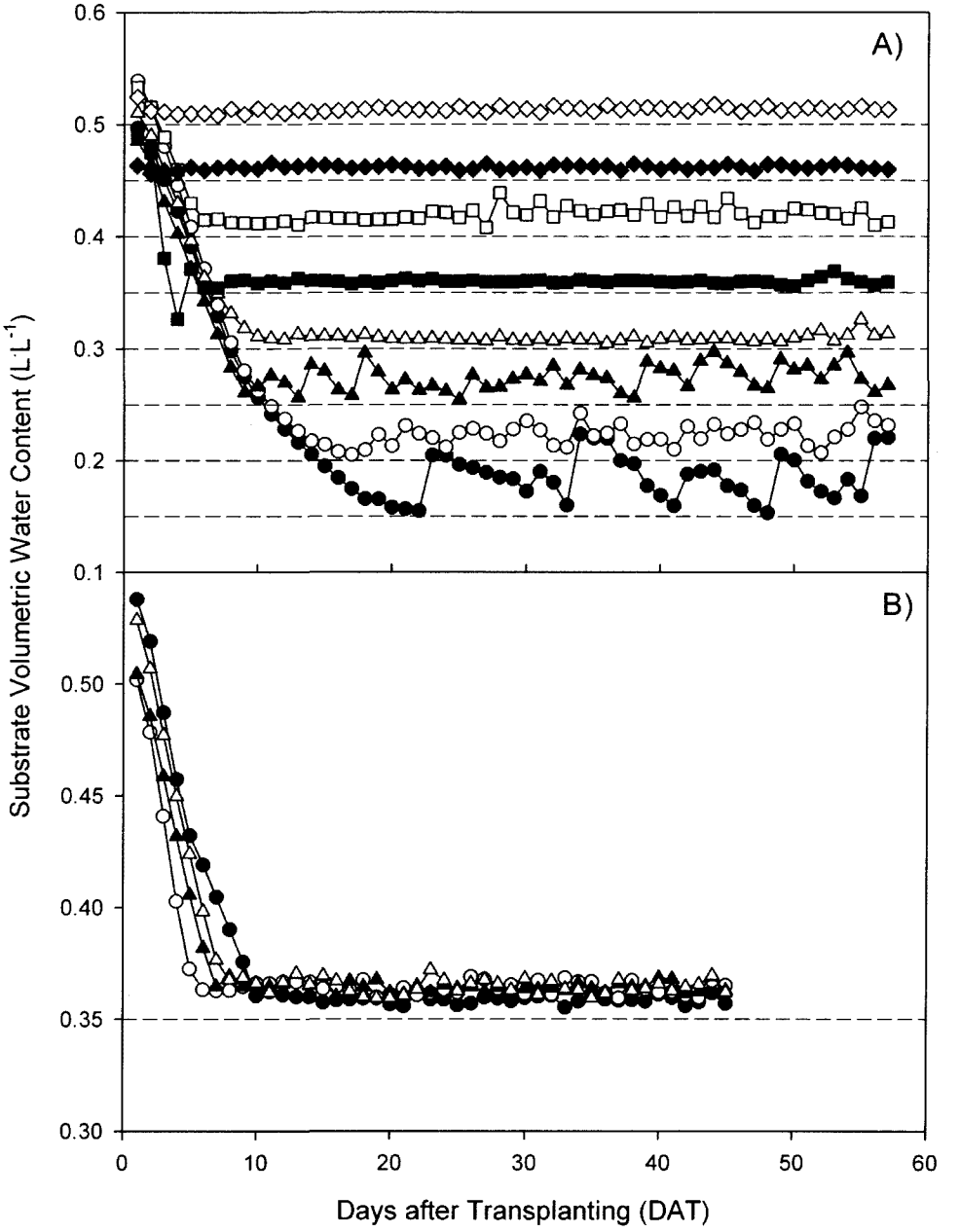

Figure 3.1. Daily average substrate volumetric water content over time during the water study (A) and the light study (B).

been observed in petunia, purple cone flower, *Gaillardia aristata* Pursh, *Lavandula angustifolia* P. Mill., penstemon, and *Penstemon* x *mexicali* Mitch. 'Red Rocks' (penstemon 'Red Rocks') indicate that plants may acclimate to drought stress over time (van Iersel, unpublished data, Zollinger et al., 2006). This may have also been the case for heuchera, however, Ψ_W was not measured during earlier stages of the experiment. Changes in relative root mass and hydraulic conductance may likely account for the ability of plants exposed to the lower set points to maintain leaf water status (Jones, 2007; Poorter and Nagel, 2000, Zollinger et al., 2006).

g_s did not differ among plants grown at θ ranging from 0.15 to 0.50 $L \cdot L^{-1}$ (Table 3.1). Quite often, the most influential limitation to photosynthesis during periods of water stress is the reduced diffusion of CO_2 to the site of carboxylation. The two major factors responsible for limited CO_2 diffusion during periods of water stress are g_s and mesophyll conductance (g_m) (Flexas et al., 2008; Kramer & Boyer, 1995). Stomatal response to water stress is species dependent. Further, g_s changes according to duration and intensity of the water stress applied, and can be influenced by previous exposure to water deficit (Pospíšilová and Dodd, 2005). Again, plants in the lower θ set points may have developed morphological and biophysical characteristics such as increased relative root mass and increased hydraulic conductivity that could have allowed them tolerate reduced θ without a subsequent reduction in stomatal aperture (Jones, 2007; Poorter and Nagel, 2000, Zollinger et al., 2006).

It was reported in a review by Flexas and Medrano (2002) that metabolic impairment occurs primarily when g_s is less than 0.05-0.1 $mol \cdot H_2O \cdot m^{-2} \cdot s^{-1}$, regardless of species and leaf water status. This supports our observation that A_N and Vc_{max}, J_{max}, and

	Substrate Volumetric Water Content (θ) $L \cdot L^{-1}$							
	0.15	0.20	0.25	0.30	0.35	0.40	0.45	0.50
A_{net} ($\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$)	8.5a ± 0.36	8.2a	8.9a ± 0.09	6.9a	10.2a	9.2a ± 0.33	9.3a ± 0.9	9.3a ± 0.12
Vc_{max} ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	16.0	12	12.8	10.8	16.4	16.4	12.8	15.6
J_{max} ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	67.8	59.8	61.7	54.3	79.1	75.8	65.0	71.6
R_d ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	-1.31	-1.02	-0.73	-1.12	-1.06	-1.42	-0.85	-1.29
Fv/Fm	0.76a ± $1.6e^{-2}$	0.77a ± $1.2e^{-2}$	0.77a ± $1.6e^{-2}$	0.76a ± $1.5e^{-2}$	0.76a ± $1.6e^{-2}$	0.77a ± $1.8e^{-2}$	0.77a ± $1.8e^{-2}$	0.80a ± $3.5e^{-3}$
g_s ($mol \cdot m^{-2} \cdot s^{-1}$)	0.13a ± $3.0e^{-2}$	0.24a	0.17a ± $2.9e^{-2}$	0.18a	0.22a	0.16a ± $3.6e^{-2}$	0.15a ± $1.5e^{-3}$	0.19a ± $2.1e^{-2}$
E ($mol \cdot m^{-2} \cdot s^{-1}$)	1.17a ± 0.39	1.97a	1.64a ± 0.21	1.52a	.	1.22a	1.65a ± 0.15	1.46a ± 0.12
C_i/C_a	0.65a ± $5.8e^{-2}$	0.83a	0.72a ± $4.3e^{-2}$	0.82a	0.76a	0.67a	0.70a	0.75a

Table 3.1. Influence of substrate water content on leaf gas exchange and fluorescence in *Heuchera americana* 'Dale's Strain'

R_d were not influenced by θ (Table 3.1). Figure 3.2 also shows carbon dioxide response curves did not reflect differences among the various θ. Similarly, A_N of *Boltonia asteroides* (L.) L'Hér (boltonia), *Rudbeckia triloba* L. (three-lobed coneflower), petunia, and *Plumbago auriculata* Lam. (plumbago) were not affected by θ (Niu et al., 2006; Prevete et al., 2000). Whole canopy A_N of annual salvia, vinca, petunia, and impatiens also did not differ among θ, ranging from 0.15-0.32 $L \cdot L^{-1}$ (Nemali and van Iersel, 2008). Some studies have demonstrated that water stress can influence metabolic function (Niu et al., 2006). Care should be taken when comparing plant response to prolonged regulated deficit irrigation to responses in plants exposed to short term water deficits, such as Niu et al. (2006). Both types of water stress investigations may be valid, but they can be influenced by factors other than the current θ, such as the degree to which the plant under water stress has developed various drought acclimation characteristics.

There was a positive correlation ($P<0.0001$; $r^2=0.85$) between g_s and the relative amount of internal CO_2 (C_i) to CO_2 surrounding the leaf (C_a) (C_i/C_a), while A_N was found to be not correlated C_i/C_a. This reflected that g_s was the driving factor influencing the concentration of CO_2 available inside the leaf rather than the demand for CO_2 by A_N (Table 3.1).

Water use efficiency in terms of shoot biomass accumulation per unit of water applied (WUE_I) increased with decreasing θ (Fig. 3.3). The total volume of water applied over the duration of the experiment was positively correlated with the θ set point ($P<0.0001$; $r^2=0.74$), ranging from 2.6L (± 0.10) in substrates maintained at a θ of 0.15 $L \cdot L^{-1}$ to 5.0L (± 0.08) at a θ of 0.5 $L \cdot L^{-1}$ (Garland et al., 2009). WUE_I of *Gaura lindheimeri* Engelm. & Gray increased with decreasing θ when plants were irrigated

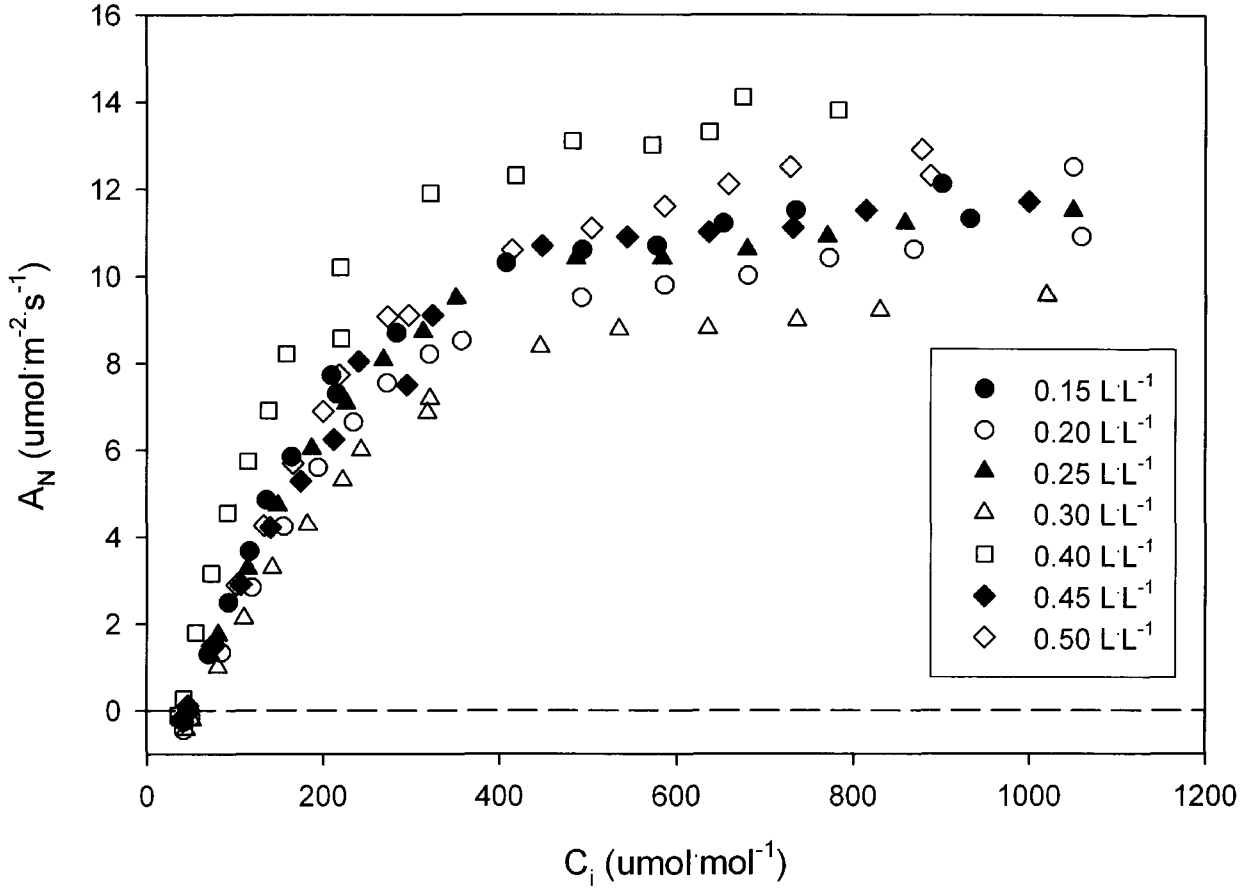

Figure 3.2. Carbon dioxide response curves for *Heuchera americana* 'Dale's Strain' grown under different substrate volumetric water contents.

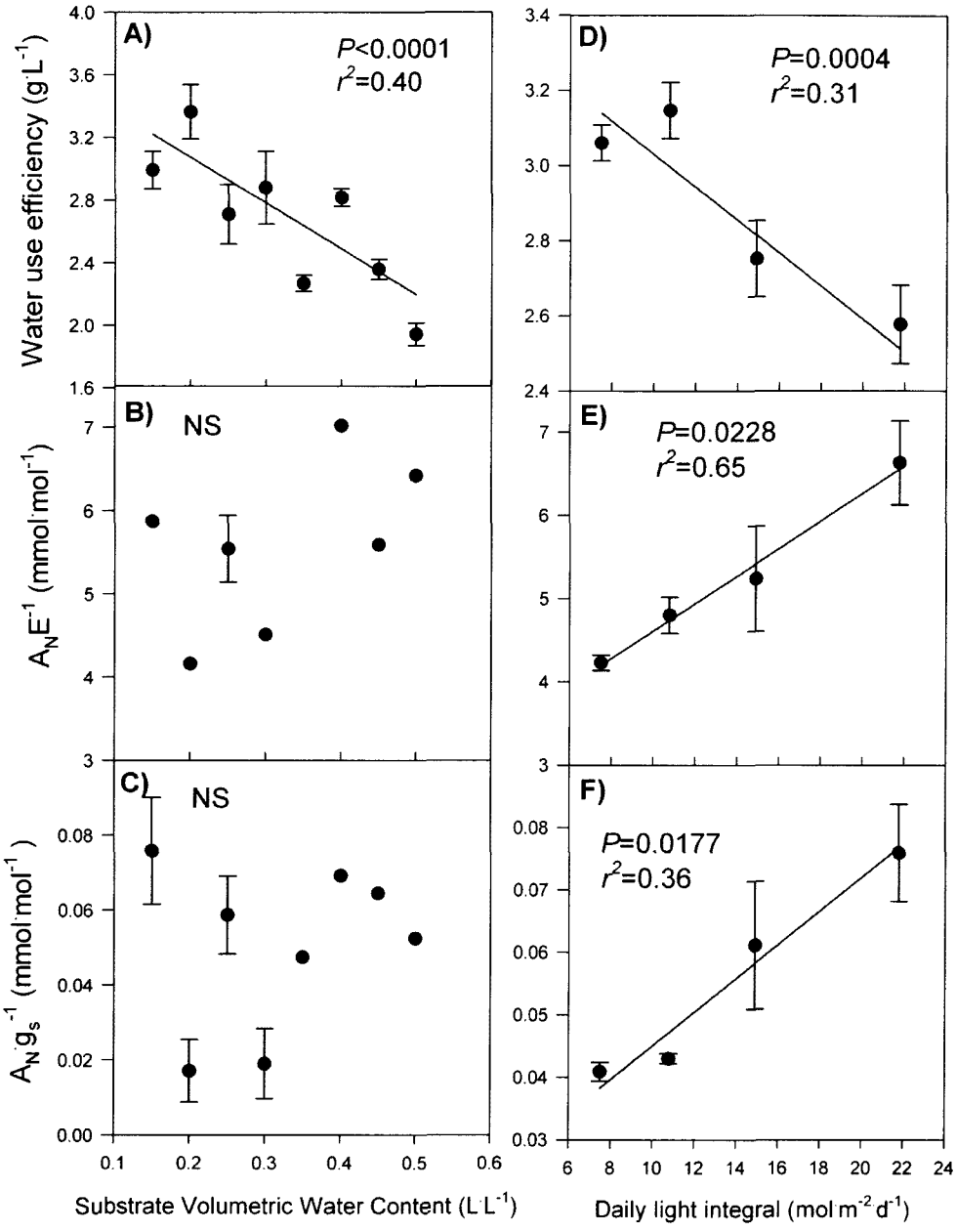

Figure 3.3. Influence of substrate water content and daily light integral on three different measures of water use efficiency.

using similar methods (Burnett et al., 2008). Irrigation based measures of WUE often include water lost to inefficient irrigation practices such as those that result in containers being overwatered yielding leachate or water loss between containers. The automated irrigation system used in this study yielded no leachate, therefore, the WUE_I calculated represented the precise amount of water applied using one of the most efficient irrigation practices available.

Neither physiological metric of water use efficiency (WUE_E or WUE_{gs}) was influenced by θ (Fig. 3.3). While WUE_{gs} increased with decreasing θ in ornamental crops such as impatiens, salvia, and vinca; it did not change among set points for petunia. WUE_{gs} values were similar to those provided for other bedding plants (Nemali and van Iersel, 2008). Kramer and Boyer (1995) mention that the relationship between WUE_{gs} and WUE_I can be poor because of factors influencing dry matter accumulation that may not be reflected in instantaneous gas exchange measures. Factors confounding the apparent WUE_I may include differences in dry matter allocation, dark respiration rates, changes in stomatal aperture throughout the day, and differences in stomatal aperture across a single leaf surface (Kramer and Boyer, 1995).

Fluorescence values indicating the apparent quantum efficiency of photosystem II (Fv/Fm) for all θ set points (Table 3.1) were comparable to those observed in heuchera grown in open field plots where the DLI likely ranged from 40-45 $mol \cdot m^{-2} \cdot d^{-1}$ (Korczynksi et al., 2002; Skillman and Osmond, 1998). Plants grown under an oak-hickory stand, where the DLI was approximately 1-2 $mol \cdot m^{-2} \cdot d^{-1}$, had significantly higher Fv/Fm values around 0.82 (Skillman and Osmond, 1998). Relatively low Fv/Fm values are not normally observed in plants exposed to water stress alone (Sánchez-Blanco et al.,

2009; Starman and Lombardini, 2006), but are often observed when water stress occurs in conjunction with high light (Jones, 1992). The mean DLI recorded for this study was 22 $mol \cdot m^{-2} \cdot d^{-1}$.

3.4.3 Experiment 2: Light

Heuchera was able to survive light levels up to 21.8 $mol \cdot m^{-2} \cdot d^{-1}$, but plants were not able to increase photosynthetic capacity to utilize the additional light received. Net photosynthetic rates did not differ among light treatments, nor did most of the estimates of photosynthetic capacity derived from light response curve such as quantum efficiency (*QE*), dark respiration (R_d), light compensation point (LCP), and maximum photosynthetic capacity (A_{max}) (Table 3.2). Fluorescence values for all DLIs were similar to those observed in heuchera plants growing in open field conditions (Table 3.2) (Skillman and Osmond, 1998). Other estimates of non-stomatal limitations to photosynthesis including carboxylation efficiency (V_{cmax}) and light saturated rate of electron transport (J_{max}) were statistically similar among the highest and lowest DLIs (Table 3.2). The possibility that mesophyll conductance (g_m) may also be influenced by light should be mentioned here. Traditional changes in leaf structure and chloroplast movement in response to different levels can influence g_m which could result in inaccurate estimations of Vc_{max} and J_{max} (Flexas et al., 2008).

g_s decreased with increasing DLI (P=0.0362, r^2=0.30) (Table 2). Many C_3 plants increase g_s in higher light levels. As mentioned in the water discussion, stomatal behavior may also be influenced by other environmental factors such as temperature or vapor pressure deficit (Kramer and Boyer, 1995). However, air temperatures did not

	Daily Light Integral ($mol \cdot m^{-2} \cdot d^{-1}$)			
	7.5	10.8	14.9	21.8
A_{net} ($\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$)	9.71a ± 0.30	11.0a ± 0.41	9.47a ± 0.51	9.11a ± 0.49
QE	0.14a ± $9.4e^{-3}$	0.15a ± $3.8e^{-3}$	0.13a ± $4.9e^{-3}$	0.12a ± $6.0e^{-3}$
LCP ($\mu mol \cdot m^{-2} \cdot s^{-1}$ PAR)	3.47a ± 0.73	4.01a ± 0.57	4.71a ± 0.66	4.96a ± 1.08
A_{max} ($\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$)	11.0a ± 0.32	12.4a ± 0.39	10.6a ± 0.62	10.0a ± 0.78
R_d ($\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$)	0.45a ± 0.10	0.61a ± 0.09	0.66a ± 0.11	0.58a ± 0.13
Fv/Fm	0.76a ± $1.3e^{-2}$	0.77a ± $0.6e^{-2}$	0.77a ± $0.9e^{-2}$	0.73a ± $0.8e^{-2}$
Vc_{max} ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	19.3a ± 0.39	.	.	20.8a ± 0.86
J_{max} ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	102.0a ± 1.2	.	.	105.2a ± 3.7
C_i/C_a	0.79a ± $0.8e^{-2}$	0.79a ± $0.5e^{-2}$	0.78a ± $2.7e^{-2}$	0.71a ± $2.0e^{-2}$
g_s ($mol\ H_2O \cdot m^{-2} \cdot s^{-1}$)	0.24a ± $5.5e^{-3}$	0.26a ± $9.3e^{-3}$	0.21a ± $3.3e^{-2}$	0.15a ± $2.3e^{-2}$
E ($mol\ H_2O \cdot m^{-2} \cdot s^{-1}$)	2.30a ± 0.14	2.38a ± 0.35	2.18a ± 0.66	1.57a ± 0.44
Chlorophyll (SPAD units)	32.9a ± 0.54	30.3ab ± 0.54	27.7bc ± 0.43	26.1c ± 0.53

Table 3.2. Influence of daily light integral on leaf gas exchange, fluorescence, and chlorophyll concentration in *Heuchera americana* 'Dale's Strain'

differ among treatments. Midday reduction in stomatal aperture has been observed in several species and might be more likely to occur in high light conditions (Xu and Shen, 2005). Measures of transpiration (E) in plants under higher DLIs had lower rates of water loss at higher light levels (P=0.0290, r^2=0.63) most likely due to the similar trend in g_s (Table 3.2).

Previous studies demonstrated that *Heuchera americana* possesses the capacity to acclimate to seasonal changes in light as well as changes imposed in the laboratory (Skillman et al, 1996; Skillman and Osmond, 1998). DLIs commonly experienced by heuchera in its native habitat range from approximately 1 $mol \cdot m^{-2} \cdot d^{-1}$ in the summer, when the tree canopy above has closed, to roughly 11 $mol \cdot m^{-2} \cdot d^{-1}$ in the winter, after trees have dropped their leaves. The three highest treatments applied in this investigation (10.8, 14.9, and 21.8 $mol \cdot m^{-2} \cdot d^{-1}$) were towards the top of the range of DLI observed in native sites. Light response curves and carbon dioxide response curves indicate no further acclimation to higher light levels (Fig. 3.4).

One possible explanation for the lack of photosynthetic acclimation to higher light levels is associated with the relatively slow growth rate of the species. Increasing light without a corresponding increase in carbohydrate sink strength may have resulted in the accumulation of carbohydrates in the foliage. Carbohydrate accumulation may play a role in regulating the capacity for plants to increase photosynthesis in high light situations (Paul and Foyer, 2001). Supporting this theory is the observation that shoot dry weight for heuchera reaches saturation at a DLI of 10.8 $mol \cdot m^{-2} \cdot d^{-1}$ (Garland et al., 2009). Rothstein and Zak (2001) mention the possibility that adaptations associated with leaf longevity may also play a role in the capacity for a plant to acclimate to higher light

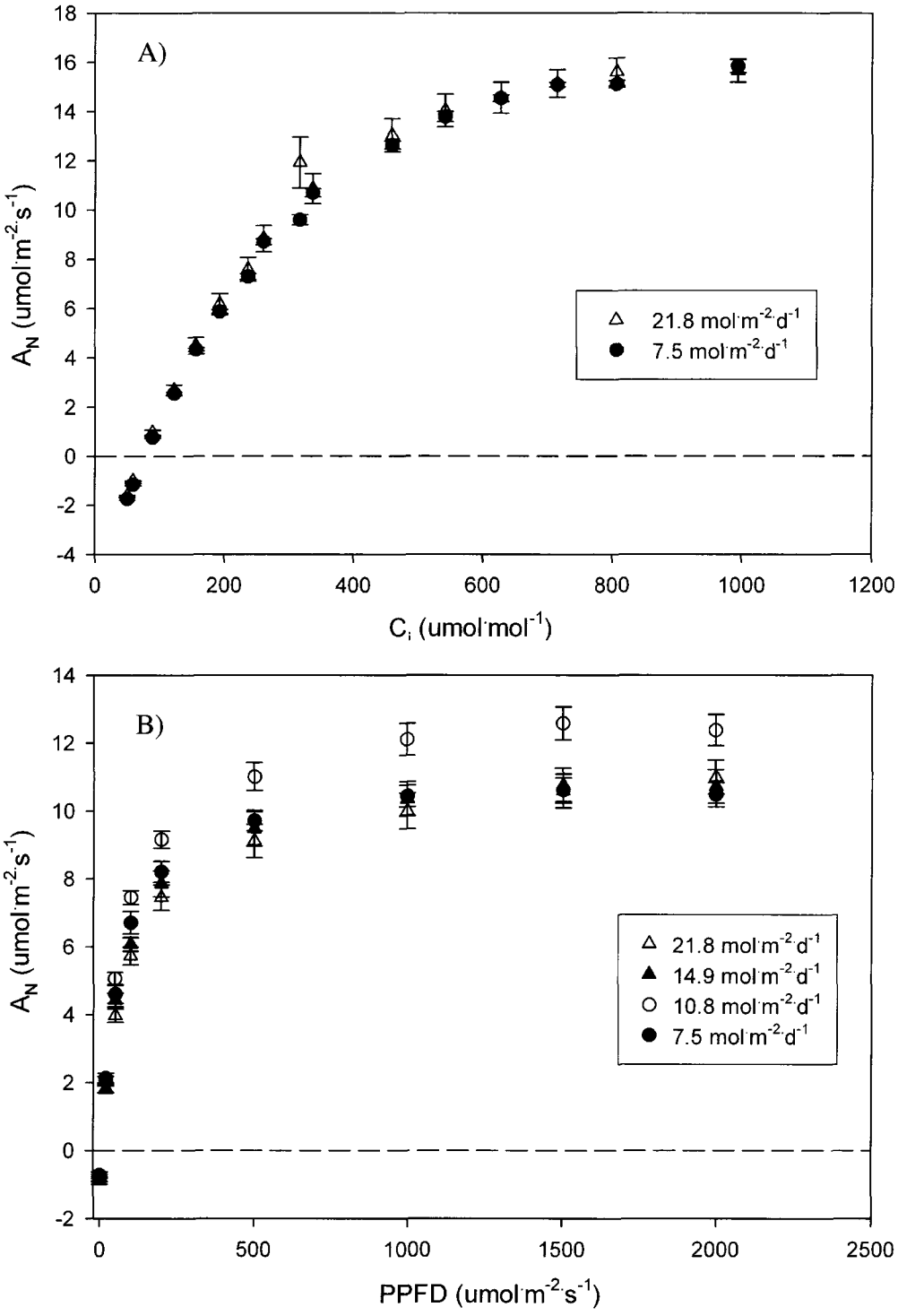

Figure 3.4. Carbon dioxide response (A) and light response (B) curves for *Heuchera americana* 'Dale's Strain' grown under four daily light integrals.

levels. Plants with more frequent leaf turnover, such as *Viola pubescens* Ait. (downy yellow violet), are more capable of adjusting photosynthetic capacity throughout the year compared to plants with more persistent foliage, such as *Tiarella cordifolia* L. (foamflower) (Rothstein and Zak, 2001).

SPAD measurements, which correlate to chlorophyll concentration, appeared to have a negative curvilinear response to increasing DLI ($P<0.0001$, $R^2=0.21$) (Table 3.2). Similarly, other researchers have observed that chlorophyll concentration increases concentration in plants exposed to lower light levels for a number of species (Nemali and van Iersel, 2004, Rothstein and Zak, 2001; Skillman et al., 1996). This adaptive trait generally enhances the light capturing capacity of plants under limiting light levels, allowing them to sustain net photosynthetic rates under lower light conditions. Although the trend observed here is one that is expected of plants exposed to different light levels, it should also be noted that increased reflectance in higher light levels may have influenced this reading. One of the main ornamental traits of *H. americana* 'Dale's Strain' is a silver appearance observed between leaf veins. SPAD meter estimates of chlorophyll content are based on optical analysis. Some species, such as *Pulmonaria officinalis* L. (lungwort), increase leaf reflectance in response to higher light levels (Esteban et al., 2008). If heuchera follows the same trend as lungwort, the silvering characteristics may have been less significant under lower light levels, which would also result in a lower SPAD reading.

Lower transpirational water loss (E) without a corresponding change in A_{net} resulted in greater WUE_E for plants under higher DLIs (Fig. 3.3e). It was also noted that WUE_{gs} was positively correlated with DLI ($P=0.0177$, $r^2=0.36$) (Fig. 3.3f). Differences

in E and g_s would normally lead to a corresponding discrepancy in θ in most experimental situations assessing plant response to differing light levels. The potential interaction of reduced water availability in the light experiment was of no concern here because θ was accurately managed at a level of 0.35 $L \cdot L^{-1}$ for all light treatments throughout the course of this investigation, regardless of differences in transpirational demand. Thus providing a more precise understanding of how light, alone, influences plant WUE.

The two previously mentioned physiological measures of WUE conflict with those calculated for WUE_I, which suggest that WUE_I decreases with increasing DLI (Fig. 3.3d). Lower WUE_I at the higher light levels was likely due to increased evaporative demand directly from the substrate, which subsequently triggered the irrigation system to turn on more frequently. The total volume of water applied supports this explanation, as it had a curvilinear association with DLI ($P<0.0001$, $R^2=0.48$). Other possible factors that could have influenced the WUE_I trend, such as increased shoot dry weight in higher light treatments or greater total E loss from higher total leaf areas were both found to be non-significant (Garland et al., 2009). To summarize, WUE in terms of water applied was less efficient in higher light levels, but on a physiological level, plants were using water most efficiently at higher DLIs.

3.5 Conclusion

Native *H. americana* is most commonly observed in rocky, dry woodland settings (Cullina, 2000), which helps explain its ability to tolerate low θ. Heuchera was able to maintain leaf water potentials and photosynthetic activity throughout the range of θ

examined. Management of leaf water status appears to be more likely morphological in nature or associated with changes in hydraulic conductivity, rather than managed by reduced stomatal aperture or osmotic regulation. Acclimation to regulated deficit irrigation allowed plants to sustain the same photosynthetic capacity across all θ set points.

Although heuchera is known to adjust its photosynthetic capacity according to seasonal changes in light in its native habitat, light level had no impact on leaf photosynthesis among the range of DLIs examined in this study.

WUE_I was positively correlated with both light and water availability. Physiological measures of WUE, WUE_{gs} and WUE_E, were not statistically different among any of the water treatments and completely conflicted with WUE_I results in the light study. Reduction in WUE_E and WUE_{gs} in heuchera growing in higher DLI treatments was likely due to higher leaf temperatures and greater vapor pressure deficits. This finding supports the notion that the factors influencing various measures of WUE should be well understood when comparing different WUE results.

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CHAPTER 4:

INFLUENCE OF DAILY LIGHT INETRAL ON COLEUS MORPHOLOGY AND LEAF VARIEGATION

4.1 Abstract

Solenostemon scutellarioides (L.) Codd (coleus) has been traditionally recommended as a shade plant, but, many cultivars are also suitable for full sun. To determine the influence of daily light integral (DLI) on the morphology and leaf variegation of two coleus cultivars, 'Kong Red' and 'Wizard Coral Sunrise' potted plants were grown under four DLIs: 2.9, 3.8, 5.8, and 10.0 $mol \cdot m^{-2} \cdot d^{-1}$. Both cultivars showed 4.2 fold increases in shoot dry weight as DLI increased from 2.9 to 10.0 $mol \cdot m^{-2} \cdot d^{-1}$. 'Kong Red' coleus at the highest DLI were 25% taller and 21% wider than those grown under the lowest DLI and 'Wizard Coral Sunrise' coleus were, similarly, 22% taller and 18% wider when grown under the highest DLI examined. 'Kong Red' had 3.6 times as many branches and 'Wizard Coral Sunrise' had over twice as many branches when grown under 10.0 $mol \cdot m^{-2} \cdot d^{-1}$ compared to those grown under the lowest DLI. Leaf counts for both cultivars were 64% greater when grown under the highest DLI compared to those produced under the lowest DLI; leaf area for both cultivars was also positively correlated with DLI. Leaves of both cultivars had significantly more green area, i.e. less variegation, when grown under lower light levels. Overall, both cultivars exhibited a more dense growth habit and greater degree of variegation when grown under the highest DLI. Therefore, we recommend growing 'Kong Red' and 'Wizard Coral Sunrise' coleus under a minimum DLI of 10.0 $mol \cdot m^{-2} \cdot d^{-1}$.

4.2 Introduction

Solenostemon scutellariodes (L.) Codd (coleus) is a diverse and enormously popular ornamental foliage plant that has been enjoyed by plant enthusiasts for over a century (Armitage, 2001; Rogers and Hartlage, 2008). The uniquely colored foliage of coleus can be found throughout the landscape in garden beds, containers, and hanging baskets. Leaves of coleus are either a single color or are a distinctly variegated combination of two or more colors including burgundy, green, pink, coral, yellow, orange, and dark purple. Although traditionally recommended as a shade plant, many newer cultivars of coleus have been reported as being suitable for full sun (Armitage, 2001; Rogers and Hartlage, 2008; Stack, 2009).

Daily light integral (DLI), the cumulative photosynthetically active radiation a plant receives over a 24 h period, influences various plant characteristics in a number of crops. For instance, increasing DLI decreased time to flower and increased flower number for *Viola* × *wittrockiana* Gams. (pansy) and *Cyclamen persicum* Mill (cyclamen) (Niu et al., 2000; Oh et al., 2009). Shoot dry mass of *Celosia argentea* var. *plumosa* L. 'Gloria Mix' (cockscomb), *Impatiens walleriana* Hook. 'Accent Red' (impatiens), *Tagetes patula* L. 'Bonanza Yellow' (marigold), and total dry weight (shoot and root) of *Begonia semperflorens-cultorum* Hort. 'Cocktail Vodka' (wax begonia) was greater when plants were grown under higher DLIs (Nemali and van Iersel, 2004; Pramuk and Runkle, 2005). Fausey et al. (2005) reported that higher amounts of light resulted in improved visual quality (height, flower color, lateral branching, foliage color) of *Achillea millefolium* L. 'Red Velvet' (yarrow), *Gaura lindheimeri* Engelm. & Gray 'Siskiyou Pink' (gaura) and *Lavandula angustifolia* Mill. 'Hidecote Blue' (English lavender).

The most favorable DLI for plant production depends on the crop being grown. Minimum DLI recommendations for high light adapted crops such as yarrow, gaura, and English lavender range from 15-20 $mol \cdot m^{-2} \cdot d^{-1}$ (Fausey et al., 2005). Whereas, the recommended DLI for English ivy (*Hedera helix* L.), a low light adapted crop, is 5.4 $mol \cdot m^{-2} \cdot d^{-1}$ (Pennisi et al., 2005).

DLI may also influence leaf variegation. English ivy 'Gold Heart', *Epipremnum aureum* Bunt. E. pinnatum (pothos), and *Aspidistra elatior* 'Variegata' Bl. (cast iron plant) are all foliage crops that become less variegated when grown under lower amounts of light (Nam et al., 1997; Pennisi et al., 2005; Stamps, 1995). Conversely, the leaves of variegated cultivars of *Peperomia obtusifolia* L. (radiator plant) and *Dracaena sanderana* hort. Sander ex Mast. (dracaena), have more variegation when plants are grown under less light (Shen and Seeley, 1983; Vladimirova et al., 1997).

Greenhouse production of coleus occurs, most often, between the months of February and May in the United States. Mean outdoor DLIs at this time of year in Northeast range between 15 and 20 $mol \cdot m^{-2} \cdot d^{-1}$ compared to 55 to 60 $mol \cdot m^{-2} \cdot d^{-1}$ in the Southwest (Korcynski et al., 2002). Actual DLIs within a greenhouse can differ greatly depending on the structure and glazing, and transmission may be reduced up to 50% (Fisher and Runkle, 2004). Depending on local light levels and the crop being grown, growers may choose to increase DLI using supplemental lighting, or limit DLI through the use of shading materials. Both management options can be expensive to install and operate. Therefore, it is essential to understand the exact needs of the crops being grown in order to make wise decisions regarding light management.

Successful coleus sales rely on a combination of dramatic coloration and dense growth habit. To our knowledge, the light conditions required to promote these characteristics in coleus have not been reported. Therefore, the objective of this study was to determine the optimal light levels necessary to produce the most marketable coleus crop.

4.3 Materials and Methods

Two cultivars of coleus, 'Kong Red' and 'Wizard Coral Sunrise', were selected for this study for the following reasons: (1) their leaf margins were relatively flat, allowing the leaves to be more accurately scanned during variegation analysis, (2) the two cultivars represented two distinctly different color combinations (e.g. one dark combination and one pastel combination), and (3) the cultivars represented two different sun tolerance groups ('Kong Red' = tolerant and 'Wizard Coral Sunrise' = not tolerant) determined in a preliminary field trial that was conducted to assess sunscald in coleus grown in full sun (Stack, 2009). Foliage of 'Kong Red' is characterized by a deep burgundy center with a dark green margin, while 'Wizard Coral Sunrise' has a bright coral center edged with burgundy surrounded by a light green margin.

Seeds of 'Kong Red' and 'Wizard Coral Sunrise' coleus (Ball Horticultural Company, West Chicago, IL) were sown in 288 cell plug trays (6.8 mL cell volume) containing a peat-based germinating mix (Sun Gro Horticulture, Bellevue, WA) on 11 Aug. 2008. Seedlings were grown on a mist bench until they reached the four leaf stage. They received continuous liquid fertilization beginning 21 Aug. 2008 using a 75 $mg \cdot L^{-1}$ N solution (Peters EXCEL 15N-2.2P-12.45K Cal-Mag, The Scotts Co., Marysville, OH).

Coleus were transplanted into 3.8 L nursery containers filled with a peat-, bark- and perlite-based growing mix with starter fertilizer (Fafard 3B; Conrad Fafard Inc., Anderson, SC) on 1 Oct. 2008. After transplanting, continuous liquid fertilization was increased to 150 $mg \cdot L^{-1}$ N of the same fertilizer. Average daily temperatures between the dates of 26 Oct. 2008 and 26 Nov. 2008 were 20.5° C +/- 0.07° C. Plants were grown in a double-layer polycarbonate greenhouse for the entire experiment and were hand watered as needed after transplanting.

Three shade treatments (30, 60, and 90%) were provided by square (0.6 × 0.6 × 0.6 m) polyvinyl chloride (PVC) pipe structures covered with a single, double, or triple layer of commercial 30% shadecloth (K-Pro Supply; Sarasota, FL), respectively. Zero percent shade treatment plants were simply grown on the greenhouse benches without a PVC structure over them. Supplemental lighting was provided by 600 watt high pressure sodium lights (PL2000, P.L. Light Systems Inc., Beamsville, ON) from 0800 to 2000 EST. Light levels were monitored under each shade structure and on top of each greenhouse bench using quantum sensors (Model QSO-S, Apogee Instruments, Inc., Logan, UT) connected to a datalogger (CR10X, Campbell Scientific, Logan, UT). The datalogger was programmed to record instantaneous light levels ($\mu mol \cdot m^{-2} \cdot s^{-1}$) every five minutes throughout the entire investigation. DLIs ($mol \cdot m^{-2} \cdot d^{-1}$) were calculated using the mean of the instantaneous light levels in the following equation:

$$(\mu mol \cdot m^{-2} \cdot s^{-1} \times 60\ sec \cdot min^{-1} \times 60\ min \cdot hr^{-1} \times 24\ hr \cdot day^{-1}) \div 1{,}000{,}000\ \mu mol \cdot mol^{-1}.$$

Daily light integrals resulting from the four shade treatments were 2.9, 3.8, 5.8, and 10.0 $mol \cdot m^{-2} \cdot d^{-1}$ for plants covered with 0, 30, 60, and 90% shadecloth, respectively.

Total shoot height from the substrate surface to the highest point of the plant and width at widest point were measured weekly throughout the experiment. The study concluded on 26 Nov. 2008 (56 days after transplanting). At this time, final shoot height, width, and total leaf count were noted. Primary and secondary branches were also counted. Branches originating from the main stem were considered primary branches while those originating from primary branches were considered secondary branches. Primary and secondary branches were not counted until they had three or more leaves greater than 1 cm long.

Total leaf area of one representative plant of both cultivars from each experimental unit was measured using a leaf area meter (LI-3100A; LI-COR Biosciences, Lincoln, NE). The uppermost fully expanded leaf from these representative plants was scanned using a flat-bed scanner (ScanJet 5200C, Hewlett-Packard, Palo Alto, CA). Leaf color analysis of the scanned leaves was conducted in Adobe Photoshop (CS2 version 9.0, San Jose, CA) using the methods described by Li et al. (2007). Percent leaf area of a particular color region was calculated by the following equation:

(Pixel Count for Color(s) ÷ Pixel Count for Entire Leaf) × 100%.

All plants were dried in a soil drying room and shoot mass was noted.

An experimental unit consisted of one shade structure over four plants (two subsamples of each cultivar). Plants were arranged in a randomized complete block design with four blocks. Data were tested for linear and quadradic trends using general linear models and Fisher's LSD in Statistical Analysis Systems (version 9.1; SAS Institute, Cary, NC). *P*-values less than or equal to 0.05 were considered statistically significant.

4.4 Results & Discussion

4.4.1 Morphology

Both 'Kong Red' and 'Wizard Coral Sunrise' coleus were significantly larger when grown under higher DLI. Plants had greater shoot dry mass, and both cultivars showed 4.2 fold increases in shoot dry weight as DLI increased from 2.9 to 10.0 mol·m^{-2}·d^{-1} (Fig.. 4.1A). Mean shoot dry weight for 'Kong Red' was 1.85 and 7.70 g, and for 'Wizard Coral Sunrise' was 1.56 and 6.53 g, for plants grown under 2.9 and 10.0 mol·m^{-2}·d^{-1}, respectively.

The capacity for a plant to produce more biomass under higher amounts of light depends on the species, the amount of light intercepted by the plant, and the efficiency with which plants utilize captured light (Taiz and Zieger, 2006). Low to medium DLI requiring crops such as impatiens 'Cajun Red' and wax begonia increased in dry weight with DLI from 5 to 19 mol·m^{-2}·d^{-1}, but showed no further dry weight gains between 19 and 43 mol·m^{-2}·d^{-1} (Faust et al., 2005). Similar results were observed in cyclamen; plants did not have greater dry weights when grown under DLIs above 11.5 mol·m^{-2}·d^{-1} (Oh et al., 2009). Medium to high and high to very high DLI crops such as marigold (*Tagetes erecta* L. 'American Antigua Orange'), salvia (*Salvia coccinea* L. 'Lady in Red'), ageratum (*Ageratum houstonianum* L. 'Hawaii White') and petunia (*Petunia* × *hybrida*

		Kong						Wizard					
	Week	2.9	3.8	5.8	10.0	r^2	P>F	2.9	3.8	5.8	10.0	r^2	P>F
Height (cm)	3	5.6a	5.5a	5.5a	5.9a	ns	ns	5.0a	5.0a	5.5b	4.8a	0.42	0.0138
	4	7.1a	7.1a	7.6ab	8.0b	0.33	0.0264	5.5a	6.1ab	6.6b	6.4b	0.40	0.0186
	5	8.8a	9.3ab	9.8b	10.1b	0.20	0.0107	6.9a	6.9ab	8.6c	7.8b	0.42	0.0130
	6	11ab	10a	11.9bc	12.4c	0.34	0.0226	8.4a	9.1a	11.3b	11.8b	0.73	<0.0001
	7	12.6a	11.9a	12.7a	13.2a	ns	ns	10.5a	11.1a	13b	14.3b	0.69	<0.0001
	8	13.3a	13.9ab	15.4bc	16.6d	0.53	0.0003	13.2a	13.1a	16b	16.1b	0.62	<0.0001
Width (cm)	2	9.1a	8.8a	9.2a	9a	ns	ns	6.2a	6.8b	6.6ab	6.3a	0.39	0.0286
	3	13.2a	13.7ab	14.8bc	15.5c	0.40	0.0104	9.6a	10.4b	10.8b	9.6a	0.55	0.0008
	4	16.5a	17.3ab	18.1bc	18.8c	0.37	0.0179	13.6a	14.5ab	15.2b	14.1a	0.50	0.0028
	5	20.4a	22.0b	24.1c	24.8c	0.68	<0.0001	18.8a	18.9a	19.3a	18.3a	ns	ns
	6	27.3a	29.6b	31.4b	34.1c	0.64	<0.0001	24.3a	24.8a	24.4a	25.4a	ns	ns
	7	32.8a	34.4a	34.4a	38.7b	0.47	0.0013	26.9a	28.6a	28a	30.3b	0.41	0.0074
	8	34a	36.2ab	38.6bc	40.1c	0.51	0.0020	31.3a	33.1ab	34.4bc	36.1c	0.58	0.0007

Table 4.1. Weekly mean height and width of coleus (*Solenostemon scutellarioides*) grown under four daily light integrals

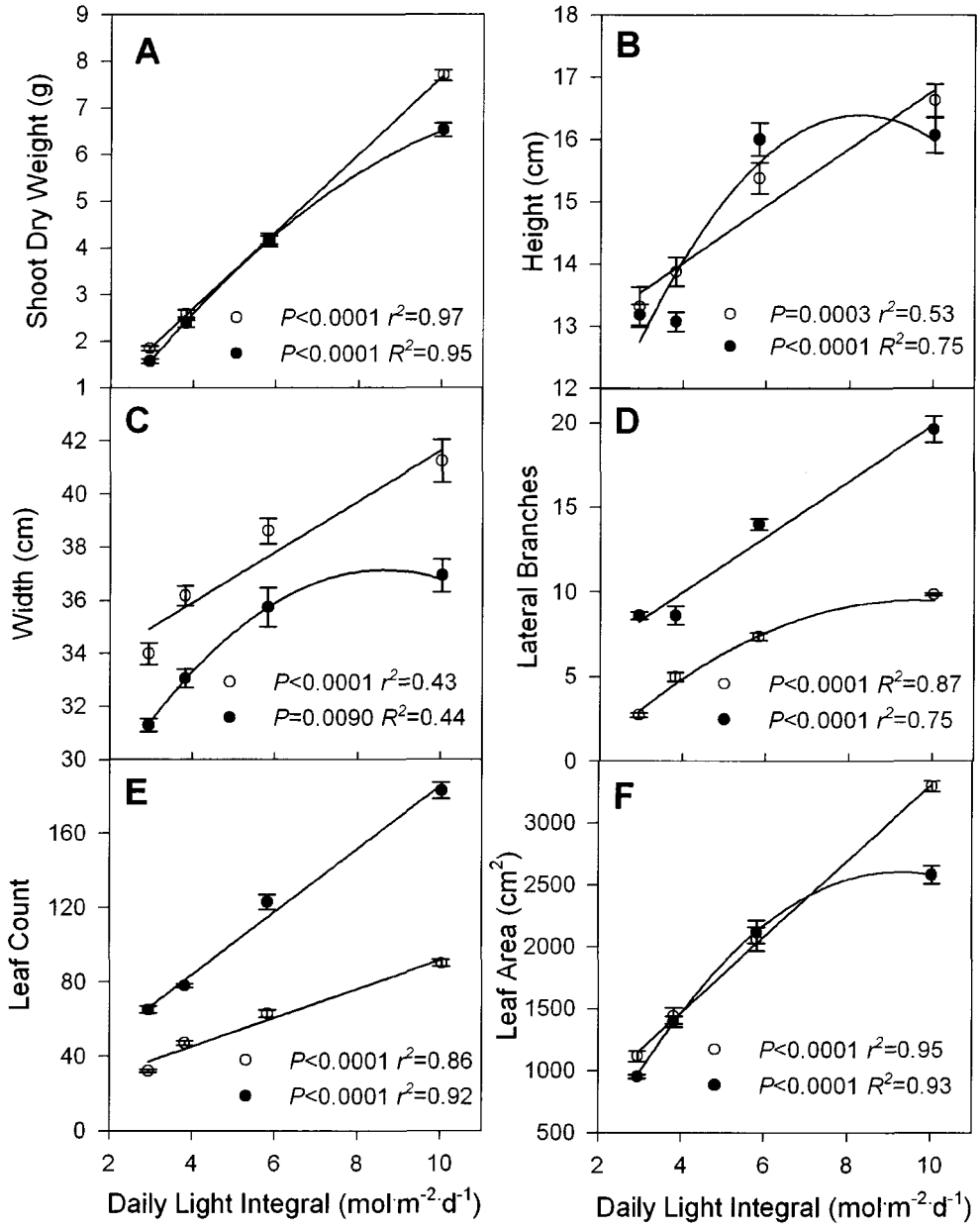

Figure 4.1. Influence of daily light integral on coleus (*Solenostemon scutellarioides*) 'Kong Red' (○) and 'Wizard Coral Sunrise' (●) shoot dry weight(A), height (B), width (C), branching (D), number of leaves (E), and total leaf area (F).

Juss. 'Apple Blossom') yield higher total dry mass with increasing DLI up to 43 mol·m^{-2}·d^{-1} (Faust et al., 2005). Corn (*Zea mays* L.), another very high DLI crop, continues to produce higher shoot dry weights with increasing DLIs up to 73 mol·m^{-2}·d^{-1} (Warrington and Norton, 1991).

Total shoot height and maximum width of 'Kong Red' and 'Wizard Coral Sunrise' coleus were greater under higher daily light integrals (Fig. 4.1B,C). This trend became apparent during weekly height measurements as early as week 3 for 'Wizard Coral Sunrise' and week 4 for 'Kong Red' (Table 4.1). Significant trends in plant width were observed after only two and three weeks in 'Wizard Coral Sunrise' and 'Kong Red', respectively (Table 4.1). 'Kong Red' coleus showed a linear positive correlation with DLI for final measures of both height and width; plants grown under the highest DLI were 25% taller and 21% wider than those grown under the lowest DLI. 'Wizard Coral Sunrise' shoot elongation and width at harvest increased quadratically among the treatments. According to means separation analysis, there was no difference in height or width between the two highest DLIs: 5.8 and 10.0 mol·m^{-2}·d^{-1}. 'Wizard Coral Sunrise' coleus grown under 5.8 or 10.0 mol·m^{-2}·d^{-1} of light were 22% taller and 18% wider compared to those grown under the lowest DLI (Fig. 4.1B,C).

Not all bedding plants grow taller and wider when grown under more light. The stretched or leggy appearance frequently observed in plants grown under suboptimal light conditions is usually more likely due to changes in the quality of light (the ratio of red:far red wavelengths) from shading by other plants; rather than the amount of light intercepted (Faust, 2003; Taiz and Zieger, 2006). Faust et al. (2005) conducted a similar study in which eight different bedding plants were grown under DLIs ranging from 5-43

$mol \cdot m^{-2} \cdot d^{-1}$. They found that only one, marigold (*Tagetes erecta* L. 'American Antigua Orange'), showed an increase in height with more light through all DLIs examined. Ageratum (*Ageratum houstonianum* L. 'Hawaii White') and petunia (*Petunia* × *hybrida* Juss. 'Apple Blossom') were both shorter under higher DLIs; while begonia (*Begonia semperflorens-cultorum* L. 'Vodka Cocktail'), salvia (*Salvia coccinea* L. 'Lady in Red') and others showed an initial increase in height up to a certain DLI and were shorter beyond that light level (Faust et al., 2005). Due the naturally low ambient light levels, we did not evaluate DLIs higher than 10.0 $mol \cdot m^{-2} \cdot d^{-1}$. 'Wizard Coral Sunrise' appears to be approaching saturation levels in the highest DLI provided in this study. However, it is difficult to say for certain how DLIs greater than 10.0 $mol \cdot m^{-2} \cdot d^{-1}$would influence plant height without testing higher light levels which may result in reduced shoot elongation.

Plants had more lateral branching at higher light levels (Fig.4.1D). Under the highest DLI, 'Kong Red' had 3.6 times as many branches and 'Wizard Coral Sunrise' had over twice as many branches compared to those grown under the lowest DLI. Of the two cultivars, only 'Wizard Coral Sunrise' had secondary branching, which was observed only at the highest two light levels (data not shown). Higher light levels often increase branching (Faust, 2003). Similar increases in lateral branching were observed in petunia, ageratum, chrysanthemum (*Dendranthema* x *grandiflorum* (Ramat.) Kitamura) and cucumber (*Cucumis sativus* L.) (Faust et al., 2005; Warrington and Norton, 1991).

The two coleus cultivars also developed more leaves and greater leaf area as DLI increased (Fig. 4.1E,F). Other researchers have observed similar responses in plant growth in a number of both high- and low-light requiring crops including chrysanthemum, radish (*Raphanus sativus* L.), corn, cucumber, wax begonia, English

ivy, and cyclamen (Nemali and van Iersel, 2004; Oh, et al., 2009; Pennisi et al., 2005; Warrington and Norton, 1991).

4.4.2 Variegation

Both cultivars showed significant changes in leaf coloration in response to their exposure to the various DLIs (Fig. 4.2 & 4.3). For the purposes of this paper, the term variegation refers to the relative amount of non-green leaf area per leaf. Leaves of both cultivars had less variegation when grown under lower DLIs. In other words, plants exposed to less light had a greater amount of green area per leaf. Increased variegation under higher light levels has also been observed in English ivy, pothos, and cast iron plant (Nam et al., 1997; Pennisi et al., 2005; Stamps, 1995).

The type of variegation observed in coleus is most likely due to non-clonal physiological changes in pigment concentration (Svoboda Pennisi, personal communication). Anthocyanins are the colored flavanoid pigments responsible for much of the red coloration observed in coleus and a number of other ornamental crops (Beckwith et al., 2004; Lamprecht et al., 1975; Oren-Shamir and Levi-Nissim, 1997). It has been reported that the concentration of anthocyanins in smokebush (*Cotinus coggygria* 'Royal Purple') and cultivars of purple fountain grass (*Pennisetum setaceum* cultivars 'Rubrum' and 'Red Riding Hood') is greater under higher light conditions (Beckwith et al., 2004; Oren-Shamir and Levi-Nissim, 1997). The relative amount of burgundy in both 'Wizard Coral Sunrise' and 'Kong Red' increased quadradically with increasing DLI (P=0.0007 and 0.0001; R^2=0.67 and 0.90, for 'Wizard Coral Sunrise' and 'Kong Red', respectively). Anthocyanins absorb a high amount of green and ultraviolet

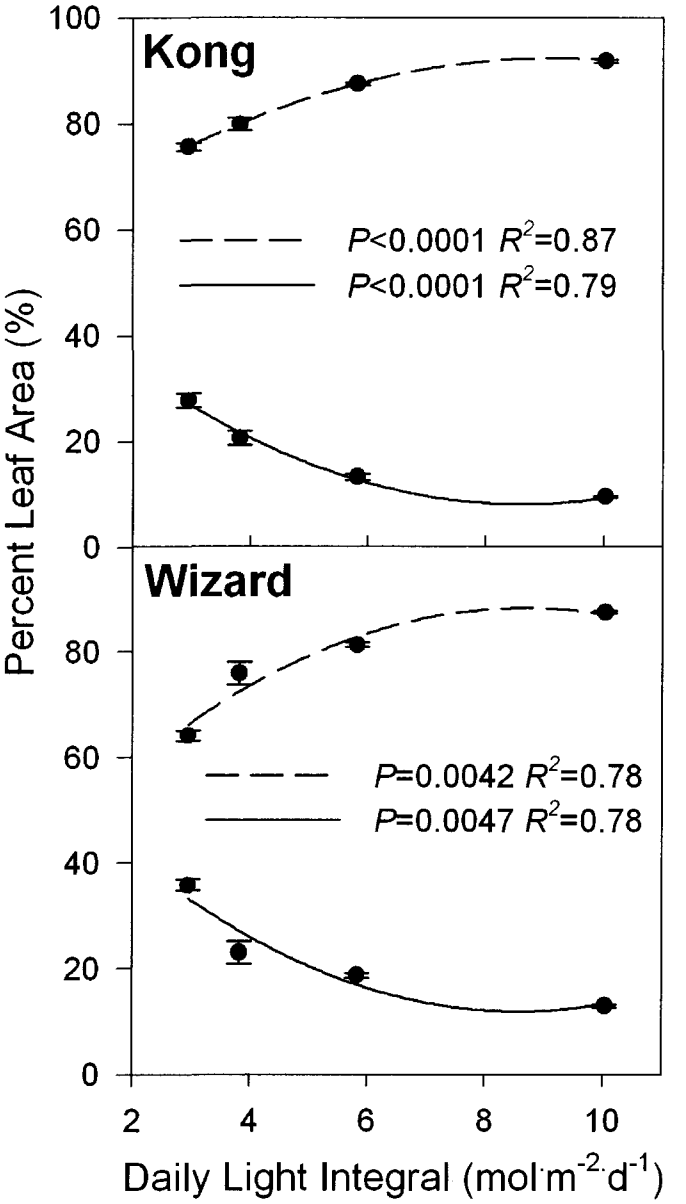

Figure 4.2. Percent green (-------) and non-green (- - - - -) leaf area of coleus (*Solenostemon scutellarioides*) 'Kong Red' and 'Wizard Coral Sunrise' grown under four daily light integrals.

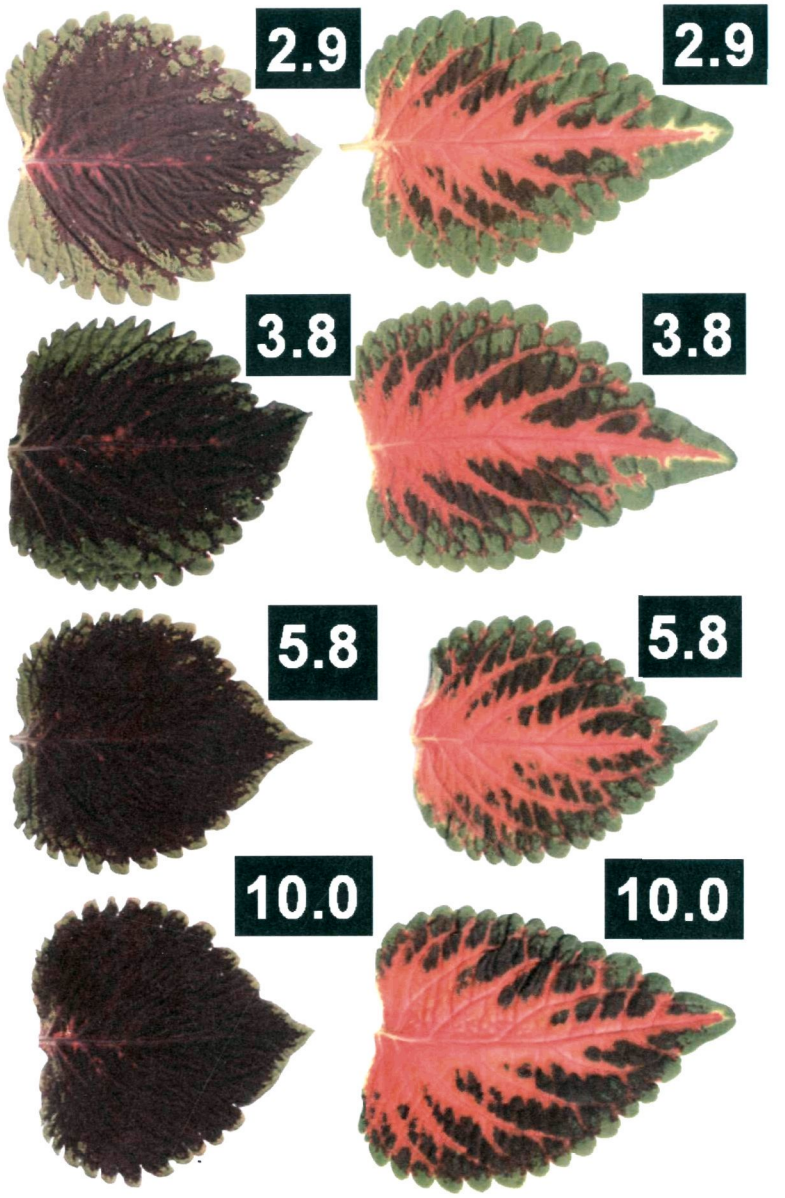

Figure 4.3. Scanned images of the uppermost fully expanded leaves of coleus (*Solenostemon scutellarioides*) 'Kong Red' (left) and 'Wizard Coral Sunrise' (right) grown under four daily light integrals.

(UV) light and a low amount of blue light while reflecting or transmitting almost all red light (Steyn et al., 2002). Under high light, anthocyanins may help prevent photoinhibition and photobleaching by screening damaging levels of light before they reach the photosynthetic apparatus (Steyn et al., 2002). Burger and Edwards (1996) observed less UVB and UVC damage in red leaf coleus compared to green leaf coleus.

4.5 Conclusion

These results indicate that 'Kong Red' and 'Wizard Coral Sunrise' coleus performed best under the highest DLI provided in this experiment. Plants were larger and more highly branched with greater leaf area under increasing amounts of light. High light also resulted in more variegated foliage. Therefore, we recommend this crop be produced under a DLI of at least 10.0 $mol \cdot m^{-2} \cdot d^{-1}$ for optimal growth and leaf coloration. Higher DLIs may or may not further enhance the production of this crop and should be the subject of further investigation. Additional studies evaluating other cultivars of coleus, changes in pigment concentration and gas exchange of coleus plants grown under various DLIs would also enhance our understanding of the versatility of this crop.

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The author grew up in Brewer, Maine receiving a B.A. in Botany from the University of Maine, Orono in 2001. Her undergraduate studies focused on forest ecology and plant systematics, which were interests that arose from experiences growing up around the woods of Maine and taking part in field research projects during her undergraduate career. The author worked several years in Maine's horticultural industry, finding a great amount of satisfaction helping customers with plant selection and answering gardening questions.

She returned to the University of Maine in the fall of 2007 to pursue a Master's degree in Horticulture in the Plant, Soil, and Environmental Sciences department with the additional goal of attaining a State of Maine secondary science teaching certification. While working towards her M.S. degree, she was awarded the Loise Cies New England Farm and Garden Fellowship and the Barrett Work Merit Fellowship in addition to two scholarships. Her goal is to teach Environmental Science and/or Agricultural Science to students of all ages by encouraging them to explore Maine's rich agricultural history and providing them with the knowledge to make future home-based agricultural endeavors successful and rewarding. Katherine is a candidate for the Master of Science degree in Horticulture from the University of Maine in December, 2009.